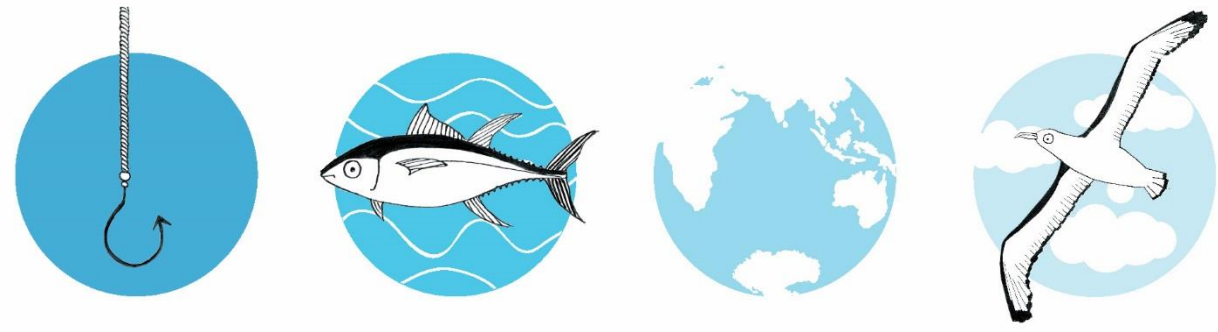

Pelagic longlines and albatross in the southern Indian Ocean:

interactions of fleet dynamics, climate change, and albatross

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Submitted in fulfillment of the requirements for the degree of Doctor of Philosophy
University of Tasmania August, 2016

Declaration of Originality

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Statement of Ethical Conduct

The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of the Gene and Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University.

Pamela E. Michael

Signed_____

Date____4 August 2016_____

Workshops and conferences attended informing research approach, and presentations resulting from research completed during candidature

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Attended Australasian Bayesian Network Modeling Society conference and pre-conference workshop, 25-28, November. The University of Tasmania, Hobart, Australia

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Oral presentation: Climate change in the southern Indian Ocean: towards projecting impacts on tuna distribution, longline fleet-dynamics, and albatross bycatch

-Seminar Series at Centre d'Etudes Biologiques de Chizé - Centre national de la recherche scientifique,8 September. Chizé, France

-3rd Climate change Impacts on Top Predators Symposium, 14-18 September Donostia-San Sebastián, Spain

-AZTI Tecnalia seminar series, 22 September. Pasaia, Spain

-2nd World Seabird Conference, 26-30 October. Cape Town, South Africa

-

2016 Poster presentation: Climate change in the southern Indian Ocean: projecting impacts of tuna distributions, longline fleet-dynamics, and albatross bycatch

-Species on the Move International Conference, Hobart, Tasmania

Authorship and Contributions

The candidate contributed between 60-70% to each of the chapters in this thesis, including acquisition of data, study design, analysis and writing. The candidate has interacted extensively with collaborators at Centre d'Etudes Biologiques de Chizé - Centre national de la recherche scientifique (CEBC-CNRS) / Universite La Rochelle (Christophe Barbraud, Karine Delord) and data providers at: Indian Ocean Tuna Commission (Miguel Herrera, Gerard Domingue), CEBC-CNRS Universite La Rochelle (Sophie Jeudi de Grissac, Henri Weimerskirch) and the British Antarctic Survey (Richard Phillips).

She has also shared datasets that she developed in collaboration with co-supervisor Geoff Tuck (Appendix B.2) with the following institutions (individuals): British Antarctic Survey (Richard Phillips), CEBC-CNRS Universite La Rochelle *(*Rémi Fay, Christophe Barbraud).

The relative author contribution of each research chapter (3-5) is summarized below, with the candidates name in **bold**

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P.E. Michael (70%)
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P.G Strutton (10%)
A. Hobday (10%)

3 Japanese and Taiwanese pelagic longline fleet dynamics and climate change in the southern Indian Ocean: a shared strategy but distinct targeting *(in preparation)*
P.E. Michael (65%)
C. Wilcox (20%)
G.N.Tuck (5%)
A. Hobday (5%)
P.G. Strutton (5%)

4 Relative impacts of the environment and fisheries bycatch on an albatross population *(in preparation)*
P.E. Michael (60%)
R. Thomson (10%)
C. Barbraud (6%)
G.N. Tuck (5%)
C. Wilcox (5%)
K. Delord (3%)
P.G Strutton (5%)
A. Hobday (5%)

5 Cumulative impacts of climate change and fleet dynamics on a southern Indian Ocean albatross colony *(in preparation)*

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A. Hobday (5%)
C. Wilcox (5%)
C. Barbraud (3%)
K. Delord (2%)
P.G Strutton (5%)

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A. Hobday: guidance processing environmental data, technical aspects, guidance on albatross data, editing and review

P.G. Strutton: guidance processing environmental data, conceptual development, presentation of manuscripts, editing and review

C. Wilcox: fleet dynamics expertise, technical and conceptual aspects of modeling approaches, technical aspects of manuscripts, editing and review

R. Thomson: expertise, guidance, and assistance implementing, interpreting, and altering the albatross population model

C. Barbraud: provided albatross demographic data and expert advice on population dynamics, guidance on the interpretation of the model, technical development, editing

K. Delord: provided albatross data and expert advice on at-sea distribution

We the undersigned agree with the above stated 'proportion of work undertaken' for each of the above published peer-reviewed manuscripts contributing to this thesis:

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Thesis Abstract

The greater Southern Ocean is vast, valuable, and vulnerable. Land masses are few and intense atmospheric and oceanographic conditions create a mosaic of logistical challenges for access. The Southern Ocean is home to unique species, including all but three of the world's albatross species and high value tunas targeted by distant-water pelagic longline fleets from multiple flagstates. Exploitation of tunas has contributed to some stocks being over-fished while indirect exploitation, through incidental bycatch, has severely impacted many albatross colonies. The impacts of climate change will further complicate the current interactions within the Southern Ocean, including those between fish, fishers, and albatross.

This thesis predicts the potential future for Southern Ocean tuna, fishers, and albatross, focusing on the Indian Ocean sector of the Southern Ocean, with some analyses in the Atlantic sector as well. The first chapter introduces the Southern Ocean, major tuna fisheries, their interactions with albatross and the potential impacts of climate change. It then describes the approach taken in this thesis. As fishers interact with both fish and albatross, the second chapter quantifies the broad-scale patterns in pelagic longline effort across both the Indian and Atlantic sectors of the Southern Ocean. This assessment reveals a strong seasonal cycle in the magnitude and distribution of effort in both sectors, generally in association with changing target species. This shift in target species is associated with both ecological (species moving to different areas) and management (start of the quota year) conditions.

The third chapter develops a novel approach to modeling fleet dynamics for distant water pelagic longline effort for Japanese and Taiwanese fleets. These models project the potential impacts of climate change on the distribution of fishing effort. From a range of effort allocation strategies that consider modelled catch per unit effort (CPUE) of four different tuna species, cost,

value, and predicted variability in CPUE in each fished area, the distribution of effort in both fleets was most similar to preferentially allocating effort into areas of low predicted variability. Using environmental parameters projecting climate change in our tuna distribution models, the models forecast an average decrease in CPUE, an increase in the average predicted variability of CPUE, and decrease in effort, related to the fishing strategy identified above; fishing in areas of low predicted variability.

The fourth chapter assesses the population dynamics of black-browed albatross (*Thalassarche melanophris*) breeding on Kerguelen Island, in the central western portion of the study area. This assessment uses an integrated population model structured by sex, age-class, breeding stage, and reproductive history and operates on a monthly, $5^{\circ} \times 5^{\circ}$ temporal and spatial scale. We quantify the bycatch of each super-fleet (fleets grouped by gear-type and reported bycatch rates) and the impact of environmental conditions on the albatross population. These analyses indicate that high bycatch in the 1990s- early 2000's decreased the population, with bycatch attributed to illegal, unreported and unregulated (IUU) demersal and non-Japanese pelagic longline effort, although the model's ability to differentiate bycatches between pelagic super-fleets is weak. In line with other studies, warmer SSTs during the incubation period favors higher productivity.

In the final research chapter, the models described above (Ch. 3 and 4) are combined to project the synergistic impacts of climate change on albatross and fleet dynamics. Reduced effort by the Taiwanese and Japanese fleets had very little impact on the population, as bycatch by pelagic longline fleets was projected to be virtually absent even with higher levels of effort.

The impact of warming SST during the incubation period increased chick survival. However, the associated increase in juvenile and immature albatross in the following years results in a density-dependent decrease in juvenile survival to age five, ultimately reducing the total number of breeding pairs in the population relative to a projection assuming no change in SST.

This work presents one of the first examples of research combining fleet dynamics with albatross population dynamics to quantify the potential impacts of climate change. The patterns identified in the broad-scale distribution of fishing effort (Ch. 2) informed the development of the fleet dynamics model (Ch. 3). After a thorough analysis of the drivers of black-browed albatross population dynamics, including the environment and bycatch of multiple fleets (Ch. 4), these projections were combined (Ch. 5).This approach demonstrates the utility of fleet dynamics models and underscores the flexibility of integrated population models when assessing how changes in multiple factors (e.g. environmental parameters, bycatch) can impact a given population in the future. These types of models can assist conservation and fisheries managers make important decisions regarding mitigation of both bycatch and the environmental impacts of climate change.

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Eric for helping me to explore, and appreciate the birds and the wine & to feel connected to the local soil and remind me how small yet striking the word is. Elaine for giving me an extremely needed place to escape to in the country. The strange combination of (in temporal order) Eric, the Axe Murderer, and Derek; you have each, in your unique ways, reminded me of what I truly value & enjoy and inspired me chase it. To whisky, shiraz, cabernet sauvignon, cold-climate sauvignon blanc, cheese, rare tortilla chips, hot-sauce, beans, local vegetables, home-made bread, native plants, birding by behavior, 'abstract' sewing and card-games.

To my tribe. My second home in Washington (state); the yoga studio and community of the Bandha Room, and the extended community in DC and the extended network of particularly special bird-os. My loved ones, departed and remaining. And for Elodie; chase what enthralls you and don't forget your headlamp.

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I did not as much 'find myself' as avoid using my PLB.

"The cure for anything is salt water – sweat, tears, or the sea" – Isak Dinessen

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1 Introduction

Once thought too vast for humans to impact, the global marine environment bears a broad footprint of human use (Halpern et al., 2008). Mounting research indicates that humans have, directly or indirectly, impacted all species (Hoegh-Guldberg and Bruno, 2010; Nagelkerken and Connell, 2015), corners (van Sebille et al., 2015) and depths of the ocean (Levitus et al., 2005). These interactions can produce unexpected impacts and management challenges resulting from complicated interactions (Audzijonyte et al., 2013; Merrie et al., 2014).

The Southern Ocean

The Southern Ocean (south of 20° S for the purposes of this thesis) is a unique and dynamic environment, interacting with all other oceans. This area encompasses shallow bathymetric features including multiple sub-Antarctic islands and broad expanses of deep ocean. The southern portion of this region is dominated by meanders of the Antarctic circumpolar current (Belkin and Gordon, 1996; Stramma and England, 1999). This area is home to a range of top predators, involved in complex foodweb dynamics (Murphy et al., 2012) and encompasses valuable tuna and billfish habitats (Arrizabalaga et al., 2014; Bestley et al., 2009; Reygondeau et al., 2012). Trawl effort generally targets scalefish, shark, and squid along continental slope or shelf habitats while demersal longline effort often targets hoki, hake, ling, and lucrative toothfish. Although some purse seine effort for tunas does occur south of 20° S, it is pelagic longline effort targeting tunas which dominates the pelagic Southern Ocean (Tuck et al., 2003).

Industrial fishing effort targeting tunas in the Southern Ocean has occurred since the 1950s (Moreno and Herrera, 2013). Tunas represent both an economical source of protein as

canned tuna, caught mainly by purse seine, often in tropical and sub-tropical waters and extremely high-grade tuna sold into the sashimi market, generally caught using longlines or pole-and-line techniques (Hamilton et al., 2011). Although greater than 60% of the total catch of major, marketed tuna species is harvested with purse seine, 14% by longline, and 11% by pole-and-line (Joseph, 2009), longline effort is more common in the Southern Ocean. The main tuna species targeted in the southern Indian Ocean are albacore (*Thunnus alalunga*; ALB), southern bluefin *(T. maccoyii*; SBT), yellowfin (*T. albacares*; YFT), and bigeye (*T. obesus*; BET). In the last decade, increasing concerns over the sustainability of tuna stocks and the number of fishing vessels has resulted in Regional Fisheries Management Organizations (RFMO) taking actions to reduce what is likely an overcapacity of fishing effort (Joseph et al., 2010; Moreno and Herrera, 2013).

In addition to tunas and the fishers who target them, the Southern Ocean is also home to albatross, with all but three northern hemisphere species using this region. Albatross are long-lived, have delayed onset sexual maturity, breed once annually or bi-annually, lay only a single egg each breeding attempt and require two adults to successfully provision a chick (Warham, 1990). They are also highly specialized to cover vast distances in search for food using an energetically efficient pattern of flight called dynamic soaring (Weimerskirch et al., 2012), with variations in body-size and wing morphology relating to wind patterns (Spear and Ainley, 1997; Suryan et al., 2008).

Interactions of fisheries and albatross

The life history of albatross makes their populations sensitive to slight changes in mortality, especially adult mortality. While fishing activities around the colony or encountered

while foraging can provide an extra source of food as birds can consume discarded catch (Arcos and Oro, 2002; Bunce et al., 2002), they may also reduce food abundance (Frederiksen et al., 2004). Additionally, a significant threat to albatross populations is fisheries bycatch; when a bird is hooked, injured, entangled and / or drowned in fishing gear (Brothers, 1991; Sullivan et al., 2006). Bycatch is thought responsible for many albatross population declines (Baker et al., 2002; Brothers, 1991; Klaer and Polacheck, 1997) and implicated as l mechanism for behavioral selection (Barbraud et al., 2013) resulting in a lower population growth rate as fast reproducing individuals were removed from the population through bycatch. Some have found support for population growth due to reduced bycatch (Robertson et al., 2014). To preserve stable and sustainable albatross populations into the future, we must understand the factors driving albatross population dynamics, and their likely future behavior.

Climate change: complicating interactions

Climate change adds an additional layer of complexity to understanding these interactions. In general, many species are predicted to shift poleward, which is in line with projected sea-surface temperature change (Poloczanska et al., 2013). Additional factors will change concurrently and are predicted to impact species distributions (Duarte, 2014; Péron et al., 2012; Weimerskirch et al., 2012). Climate change could amplify (Cheung et al., 2013; Milazzo et al., 2013) or reverse (Clucas et al., 2014) current population trends, potentially creating new paradigms (Veloz et al., 2012).

The Southern Ocean is one of the most rapidly changing pelagic environments, with changes in sea-surface temperature occurring at some of the highest observed rates (Gillett and Thompson, 2003; Levitus et al., 2005). Moreover, these changes are expected to continue

(IPCC, 2013). The response of individual species will be region-specific (Constable et al 2014) and will continue to alter foodwebs and ocean ecosystems (Hoegh-Guldberg and Bruno, 2010; O'Connor et al., 2009; Trathan et al., 2007).

The impacts of climate change on tunas and implications to fisheries have already been observed in some regions, including the Atlantic, where north Atlantic albacore and Atlantic bluefin are arriving earlier to their spawning grounds (Dufour et al., 2010). Given the importance of the tuna market (Bell et al., 2013; Hamilton et al., 2011; Robinson et al., 2010), modeling the impacts of climate change on tunas and tuna catch is an extremely active field, with recent results indicating that the response to climate change varies by species and region.

For example, focusing on the tunas targeted in the Southern Ocean, the population of albacore in the south Pacific is predicted to decrease, then increase as new spawning habitat becomes available (Lehodey et al., 2015). Regarding Bluefin tunas, a loss in habitat for adults and larva in their spawning grounds in the intra-American Seas has been predicted (Muhling et al., 2015). Yellowfin tuna catch off eastern Australia is projected to shift polewards and offshore (Dell et al., 2015) while bigeye tuna habitat in the tropical equatorial Pacific is projected to improve in the east and decline in the west, resulting in an eventual decline (Lehodey et al., 2010).

The impacts of climate and climate change on albatross are receiving increasing attention in the literature (Barbraud et al., 2012). A comparative study of Southern Ocean albatross identified environmental impacts on breeding success across species and adult survival in one species, including non-linear relationships, resulting in species-specific, contrasted population responses (Barbraud et al., 2011). Environmental variation has a very strong impact on the early life stages of albatross, where natal conditions shape the likelihood of fledging (i.e. breeding

success; Nevoux et al., 2010a) and juvenile survival (Fay et al., 2015; Nevoux et al., 2010b). In order to more accurately predict population trajectories, it is important to include other factors, particularly fisheries bycatch.

Relative impacts: fisheries and environment on albatross

While relatively few studies have combined the impacts of fisheries bycatch and environmental change, those that do have shed valuable insight into this growing field. For example, the small population size of Amsterdam albatross in the southeast Indian Ocean makes them extremely sensitive to bycatch, where a slight increase in bycatch could reverse the positive impacts of increasing SST (Rivalan et al., 2010). Contrasting the environmental sensitivity of young albatross discussed above, adult survival can be impacted by fishing effort through bycatch (Rolland et al., 2010). Using integrated population models, incorporating the concurrent impacts of bycatch and environmental variation, allows a dynamic perspective into the factors impacting albatross populations. In predicting the future environment for shy albatross, Thomson et al. (2015) identified that a combination of reduced bycatch rates and increased upwelling promoting population growth would be needed to offset the negative impacts of increased temperatures.

While these studies provide insight into the complicated relationships shaping albatross population dynamics, they generally assume the future distribution of effort is similar to the present, with alterations to the magnitude (Rolland et al., 2009b) or bycatch (Rivalan et al., 2010; Thomson et al., 2015). If albatross populations are to be sustained into the future, it is essential that we continue to refine the ability to predict the trajectory of their populations. In addition to continuing the current vein of research described above, assessing the relative impacts and

interactions of the environment and fisheries (e.g. Rolland et al., 2010; Thomson et al., 2015), a greater understanding of fisher behavior and fleet dynamics is an important gap restricting our modeling and predictive capacity. Although the response of fishers is notoriously difficult to predict (Dowling et al., 2013; Mangel et al., 2015), sometimes resulting in management having unintended consequences (Abbott and Haynie, 2012; Chan et al., 2014; Fulton et al., 2011), fleet dynamics modeling is a very active field of research.

Fleet dynamics: an opportunity for insight

Over the last two decades, a broad range of approaches has been used to model and predict fisher behavior. Bayesian approaches (Ives and Scandol, 2013), object-oriented programming (Pelletier et al., 2009), and dynamic state variable modeling (Dowling et al., 2013; Dowling et al., 2012; Gillis et al., 1995; Poos et al., 2010) have been applied to fleet dynamics. These and other studies have modelled the interaction and communication between different vessels in the same fleet (Little et al., 2004; Maury and Gascuel, 2001), developing an understanding of internal fleet dynamics, including how communication can be used to reduce bycatch (Gilman et al., 2006). Fisher behavior has been simulated to assess their potential response to external perturbations (Hamon et al., 2013), and harvest policies (Venables et al., 2009), while others have assessed the bioeconomic sustainability of fleets under different policy options (Pelletier et al., 2009). Fisher decision making (Dowling et al., 2012; Gillis et al., 1995), including risk (Dowling et al., 2013) and discarding behavior in trawl fisheries (Gillis et al., 1995; Poos et al., 2010) have also been modelled. Some have even evaluated the efficacy of economic incentives on reducing bycatch, including seabirds (Mangel et al., 2015; Pascoe et al.,

2013). This growing body of research demonstrates progress in our ability to develop and apply fleet dynamics models to progressively more complicated issues, including bycatch reduction.

Novel approaches and techniques are needed when considering industrial pelagic longline effort. Specifically, most modeling approaches require a detailed understanding of the economics of vessels (Dowling et al., 2012) or high resolution (shot by shot) effort data (Mangel et al., 2015; Pascoe et al., 2013). This prevents the application of these methods to fisheries where such information is unavailable, including much of the effort targeting tunas in the Southern Ocean.

The focus of this thesis is to develop an alternative approach to modeling the dynamics of a pelagic longline effort, allowing a more comprehensive assessment of the current and projected impacts of climate change on an albatross population. Black-browed albatross (*Thalassarche melanophrys*) breeding on Kerguelen Island in the southern Indian Ocean are the focal colony. This synergistic view of albatross population dynamics can assist conservation and fisheries managers in making important decisions regarding mitigation of both bycatch and the environmental impacts of climate change.

Japanese and Taiwanese pelagic longline fleets

The Japanese and Taiwanese fleets are two of the largest pelagic longline fleets in the Southern Ocean (Tuck 2003). Industrial pelagic longline fisheries began in the 1950s targeting Northern Hemisphere and equatorial tunas (Caton and Ward, 1996; Stobberup et al., 1998). Explorations into the Southern Ocean by Japan in the 1950s and 1960s lead to the discovery of SBT. With the development of the sashimi market and deep-freezing vessels, effort expanded

poleward, with the Japanese expansion more rapid than the Taiwanese, through the 1970s, emphasizing southern albacore species (Caton and Ward, 1996; Tuck, 2004).

The 1970s to mid-1980s were influenced by increasing fuel prices, changes in market demand, technological developments, and the declarations of Exclusive Economic Zones, which slowed or stopped the poleward expansion of effort. Effort then declined sharply between 1989 and 1990, particularly for the Japanese fleet, probably as a result of the reduced catch limits for SBT (Caton, 1991b; Caton and Ward, 1996; Tuck, 2004). Following a relatively stable period of 16 years, concerns regarding fishing capacity resulted in RFMO-lead effort to reduce fishing capacity (Moreno and Herrera, 2013). In 2006, the Taiwanese BET quota was then sharply reduced in the Atlantic (Chen, 2012). Fishing capacity for tropical tunas was held at 2006 levels, followed by swordfish and albacore capacity in 2007 (Moreno and Herrera, 2013). This coincided with a reduction in Japanese pelagic longline effort in the southern Atlantic (Fig. 1.1).

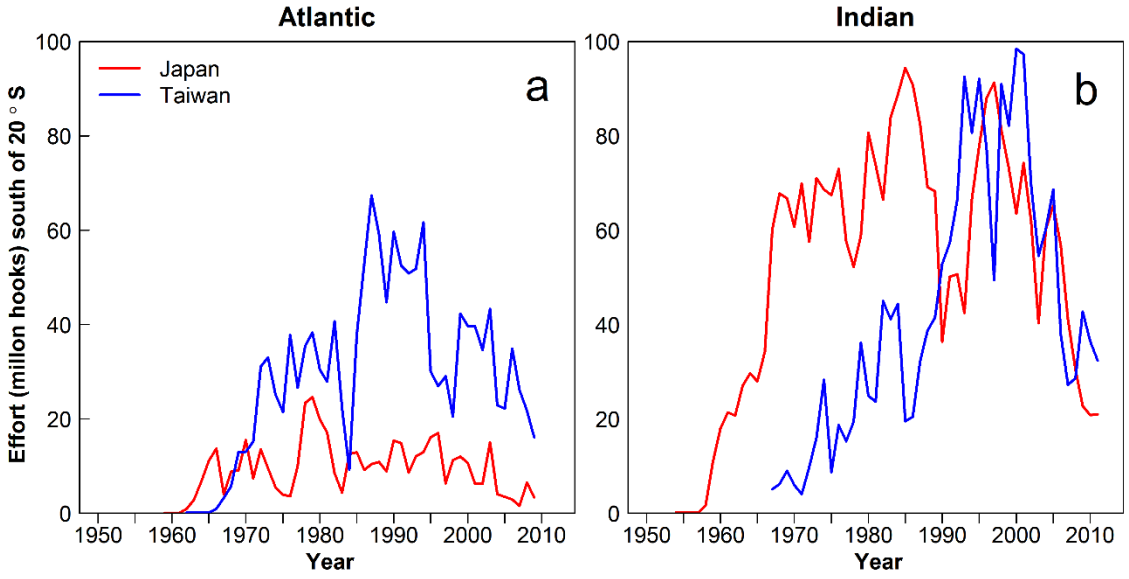

Figure 1.1 *Annual magnitude of (red) Japanese and (blue) Taiwanese pelagic longline effort south of 20S in the (a) Atlantic and (b) Indian sectors of the Southern Ocean.*

Currently, these fleets are the top two suppliers of global sashimi-grade (high value) tuna, accounting for over half of global longline catches considering all oceans (Miyake et al., 2010). The Indian Ocean south of 30° S experiences a higher magnitude of pelagic longline effort than either the Atlantic or Pacific oceans (Tuck, 2004). Both fleets target tunas, including tropical to sub-tropical YFT and BET, and sub-tropical to temperate ALB and SBT (Arrizabalaga et al., 2014; Moreno and Herrera, 2013; Reygondeau et al., 2012). The tuna vessels operating in these fleets often remain at sea for 18 months to two years (Hamilton et al., 2011) and use carrier vessels to transfer and transport about 40% of catch to markets ('transhipment'; Moreno and Herrera, 2013), while fishers remain at sea.

Black-browed albatross of Kerguelen

The black-browed albatross (BBA) colony at Cañon des Sourcils Noirs (49.40° S–70.15° E), Kerguelen Island (Fig. 1.2), Southern Indian Ocean is the ideal colony to assess the combined impacts of climate change on demography through environmental variation and bycatch. Adults are generally annual breeders, with the breeding season beginning in October when birds arrive at the colony. Following incubation, hatched chicks are then reared from January to April, while parents forage west of Kerguelen. Adults then migrate to the wintering grounds off southern Australia, soon followed by the surviving fledged chicks. Most birds remain south of Australia, somewhat concentrating northwest of Tasmania, while some travel to waters near new Zealand or south of South Africa (Delord et al., 2013).

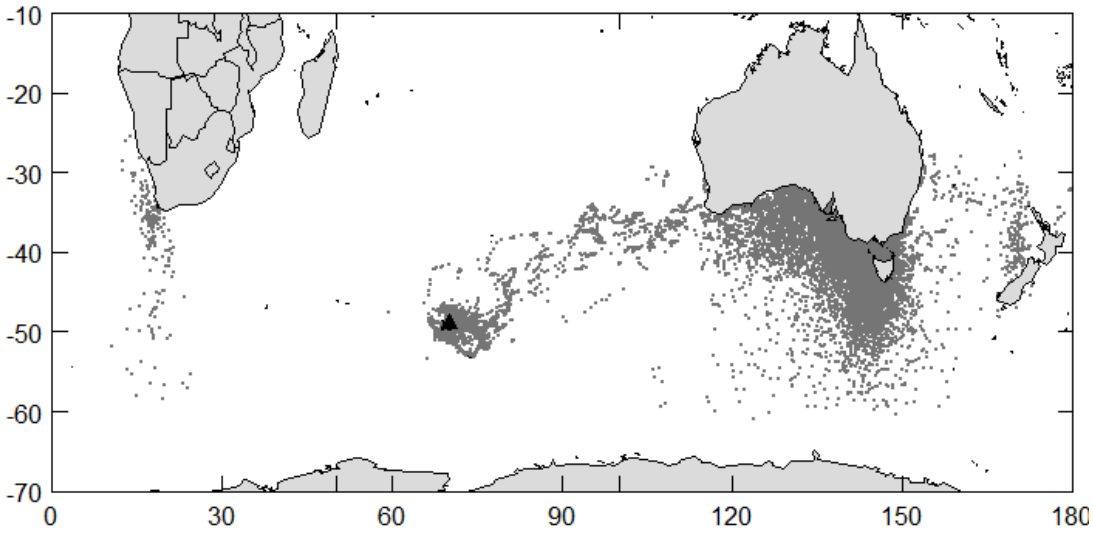

Figure 1.2 *At-sea distribution of black-browed albatross breeding on Kerguelen at Cañon des Sourcils Noirs. Colony location is indicated by the black triangle. Data are from satellite and geolocator tags deployed between 1994 and 2015.*

A long time series of demographic data, spanning over 30 years; 1979 – 2012 breeding seasons, with some data back to the 1967 season has permitted multiple studies assessing the impact of environmental variation on demography. For example, warm SST around Kerguelen during the breeding period relates to increased breeding success and adult survival (Rolland et al., 2008; Rolland et al., 2010), and population growth rate (Rolland et al., 2009b). This contrasts with the trend in the wintering grounds, where conditions suggesting low regional productivity (positive SOI) or warm SST the winter preceding breeding relate to reduced breeding success (Rolland et al., 2008; Rolland et al., 2010), population growth rate (Rolland et al., 2009b), and survival of inexperienced adults (Nevoux et al., 2007). Breeding success at the year of hatching is also related to immature survival, which could in turn result in a strong cohort effect, with cohorts hatching in low breeding success years having a lower immature survival rate (Nevoux et al., 2010b). In comparison to BBA from a colony in the Atlantic, on South Georgia, Kerguelen birds experience a lower degree of environmental variability, having higher

breeding success but lower survival than South Georgia birds (Nevoux et al., 2010a). Additionally, a study assessing climate change impacts on demography identified non-linear relationships with the environment, adding additional insight into the likelihood of breeding and complexity to their population dynamics (Barbraud et al., 2011).

Fisheries and Kerguelen BBA interactions

Of the studies evaluating the impacts of the environment and fisheries on BBA from Kerguelen, breeding success was more impacted by trawl effort, having a positive impact likely related to discards than any of the assessed environmental variables (Rolland et al., 2008). However, trawl effort during the breeding period has been inactive since 2001. A negative relationship of adult survival with longline effort in the wintering grounds and a positive relationship with warm SST during the early breeding season resulted in no net impact (Rolland et al., 2008). When compared to other species, this colony stands out from wandering and sooty albatross breeding on Crozet, and yellow-nosed albatross from Amsterdam Island as the only population where breeding success and adult survival related to a fishery and environmental covariate (Rolland et al., 2010). Given the importance of adult survival on population growth rate, future changes in either SST during the incubation period or longline effort can alter the population trajectory (Rolland et al., 2009b).

This thesis investigates the impacts of climate change on BBA population dynamics, incorporating the response of southern Indian Ocean Japanese and Taiwanese pelagic longline fleets to climate change. This requires assessing the current dynamics of these two fleets as well as historical drivers of albatross demographics. This analysis demonstrates the utility of modeling fleet dynamics, producing novel approaches and insight into complicated systems.

This thesis consists of four data chapters formatted as manuscripts. One chapter has been published, the second, third and fourth are being prepared for submission to peer reviewed journals.

2 Environmental associations of broad-scale Japanese and Taiwanese pelagic longline effort in the southern Indian and Atlantic Oceans

This chapter defines the broad-scale temporal and spatial variation in the distribution of effort for two of the largest pelagic longline fleets, and contrasts patterns in the Indian and Atlantic sectors of the Southern Ocean. The association of environmental variables at multiple temporal and spatial scales with the magnitude and distribution of effort for each fleet and region is assessed. Then, the identified associations are interpreted considering physical, ecological and management contexts. This chapter identifies a strong seasonal signal in both sectors, generally in association with changing target species. This shift in target species is associated with both ecological (species moving to different areas) and management (start of the quota year) contexts. These findings provide insight into the factors potentially driving the unique spatial distribution of these two fleets, including target species.

3 Japanese and Taiwanese pelagic longline fleet dynamics and climate change in the southern Indian Ocean: a shared strategy but distinct targeting

The third chapter builds upon the insights gained in Ch. 2 to develop fleet dynamics models for these fleets and then predicts the impacts of climate change on their distribution of effort. Specifically, we model the spatial distribution of the catch per unit effort (CPUE) of four important tuna species. From these CPUEs, we model the standard error (SE) of each modelled

CPUEs and the value of each fishing cell. Along with the relative cost of fishing in different areas, this chapter compares observed effort with that modelled by four effort allocation strategies combining the different characteristics described above. Both fleets are most associated with a strategy minimizing the modelled variability in SE of CPUE. Using environmental parameters projecting climate change in the tuna distribution models, the models predict an average decrease in CPUE summed across species, an increase in the average SE of CPUE and a decrease in the average value of a given fishing cell. Lastly, applying these results to the strategy of fishing in areas of low prediction variability projected a decrease in the magnitude of fishing effort across the region

Appendix A Additional information on data used in fleet dynamics models

This provides greater detail on the methods used to describe the catch of each fleet, the quantification of costs to the fleet, species-specific plots, and the data used to esimtate the value of each species.

4 Relative impacts of the environment and fisheries bycatch on an albatross population

The fourth chapter assesses the population dynamics of BBA breeding on Kerguelen Island in the central western portion of the study area. This comprehensive assessment uses an integrated population model structured by sex, age-class, breeding stage, and reproductive history and operates on a monthly, 5˚ × 5˚ temporal and spatial scale. This model quantifies the impact of environmental conditions and bycatch of each of five super-fleets (over 60 different fleets grouped by gear-type and reported bycatch rates) on this albatross population. These super-fleets are: Japanese mitigated pelagic longline south of 30˚ S, other pelagic longline,

demersal longline, trawl, illegal, unreported and unregulated (IUU) demersal longline. In line with other studies, warmer SSTs during the incubation period favors higher productivity. Analyses indicate that high bycatch in the 1990s to early 2000s decreased the population, with the majority of bycatch attributed to IUU demersal and non-Japanese pelagic longline effort, although the model's ability to differentiate bycatches between Japanese mitigated south of 30˚ S and other pelagic super-fleets is weak. The ability to differentiate bycatch by super-fleet and the relative impacts of environmental conditions during different periods on population dynamics provides novel insight into the factors currently driving albatross population dynamics.

Appendix B Additional information on data in used in the albatross model

An in-depth description of each type of data is provided here, including the methods used to estimate the magnitude of effort for eight fleets. This includes the deep-freezing pelagic longline effort of the following fleets: Japan, Taiwan, Korea, China, Spain, Reunion, Seychelles, and fresh longline effort for the Taiwanese fleet.

Appendix C Technical description of albatross population model

This is a detailed description of the implementation of the albatross population model.

5 Cumulative impacts of climate change and fleet dynamics on a southern Indian Ocean albatross colony

Chapter 5 combines the models developed in the previous chapters to project the cumulative impacts of climate change on Japanese and Taiwanese fleets and Kerguelen BBA. The projected reduced effort of the Taiwanese fleet and Japanese fleets had little impact on the

projected population dynamics as pelagic longline bycatch was virtually zero. Similarly, the projected bycatch of other fleets was very small, totaling around nine birds per year. Interestingly, the projected increase in SST is likely to result in a lower number of breeding pairs (~1,030) relative a continuation of the current SST (~1,100). Specifically, increasing SST during the breeding period reduces chick mortality, resulting in high numbers of fledged chicks. However, the density-dependent sensitivity of juveniles to the total number of birds in the population results in an increase in juvenile mortality, ultimately reducing the number of breeding pairs. These findings demonstrate the value of considering the impacts of climate change on fleet dynamics and albatross and the importance of density-dependence on the dynamics of some seabird populations. Despite the relatively small projected impact of bycatch on this population, the ability to test different scenarios for effort provides increased flexibility in the design and assessment of potential management approaches.

Synthesis: Implications and opportunities to manage in the face of climate change

The final chapter synthesizes the information from the earlier chapters regarding the factors impacting the distribution of fishing effort, developments in modeling fleet dynamics and the projected impacts on BBA on Kerguelen. This includes discussing the potential impacts of alternate model assumptions, with insights from other albatross populations. This section then highlights the need to continue developing the understanding of fleet dynamics, emphasizing the importance of understanding human motivations and behavior. Lastly, the importance of considering human behavior when managing natural systems is addressed, highlighting the need for collaborations across sectors.

2 Environmental associations with broad-scale Japanese and Taiwanese pelagic longline effort in the southern Indian and Atlantic Oceans

2.1 Abstract

Tunas are globally important to fisheries due to their broad distribution and high market value. However, these characteristics also complicate their management, owing to difficulties estimating population size and sustainable harvest levels. Fishing effort data can be difficult to interpret, as the magnitude and distribution of effort is the result of multiple factors, including environmental variation and targeting different species. Yet, resolving patterns in fishing effort may provide information enabling the setting of sustainable harvest levels, management of bycatch, and projection of potential responses to environmental change. To better understand the allocation of fishing effort, we evaluated Japanese and Taiwanese longline effort in the southern Indian and Atlantic Oceans and their relationships to the environment using generalized additive models. The variables evaluated included sea surface temperature, sea ice extent, climate indices, and seasonal cycles and the results were interpreted in physical, ecological, and management contexts. Our findings indicated hierarchical relationships impacting fishing effort, with a seasonal cycle an important component of most models, which we hypothesize relates to variation in species targeting. This was often followed by finer-scale environmental indices, including isotherms and sea ice, indicating region-specific dynamics impacting the magnitude and distribution of fishing effort. Additionally, effort in some regions was associated with climate indices, highlighting interannual variation. This first quantitative description of the

environmental associations of multi-species tuna fleets in the Southern Ocean is a step towards an improved understanding of fleet behavior.

2.2 Introduction

The spatial distribution of tunas varies with time and movements can span ocean-basins (Lehodey et al., 2006; Madigan et al., 2013; Martínez et al., 2006; Walli et al., 2009). The fleets that target tunas allocate effort based on these distributions, target species, management constraints, and financial motivations. Interpreting patterns in fishing data can be complicated, as the catch or catch per unit effort of a fishery is the result of multiple interacting processes (Rouyer et al., 2008). Different fleets often fish within a similar area, but can be targeting different species. Furthermore, the relationships between effort and its drivers are potentially non-linear (Gaertner and Dreyfus-Leon, 2004; Glaser et al., 2011; Maury et al., 2001). Despite these challenges, sustained use and management of fisheries resources require an understanding of the relationships between the magnitude and location of fishing effort and the physical environment. In particular, it is critical to identify shared and divergent patterns in effort when multiple fleets fish in a similar region, as changes in what drives their distribution could alter fleet behaviour and change competition for resources.

One dynamic region where high value tunas are fished by multiple flagstates is the Southern Ocean, defined here as waters south of 20° S. Industrialized distant-water pelagic longline fleets have targeted tunas in the Southern Ocean since the 1950s (Moreno and Herrera, 2013). The two flagstates with the greatest effort in this region are Japan and Taiwan, and the magnitude and distribution of fishing effort from these fleets are highly variable. For example, the southern Indian Ocean has a higher magnitude of effort than the southern Atlantic Ocean

(Fig. 2.1). Japanese effort in the Indian Ocean has east and west components while Taiwanese effort is more central (Tuck et al., 2003). In the Indian and Atlantic Oceans, Japanese fleets target southern bluefin (*Thunnus maccoyii*: SBT) and bigeye (*T. obesus*: BET) while BET and albacore (*T. alalunga*: ALB) are important target species for the Taiwanese fleet (Moreno and Herrera, 2013; SCRS, 2014). Though occasionally targeted by the Taiwanese fleet in the Indian Ocean, mature SBT are unlikely to be heavily targeted in the Atlantic, as the majority of Taiwanese effort is north of core SBT fishing grounds, which are south of 40° S (Arrizabalaga et al., 2014).

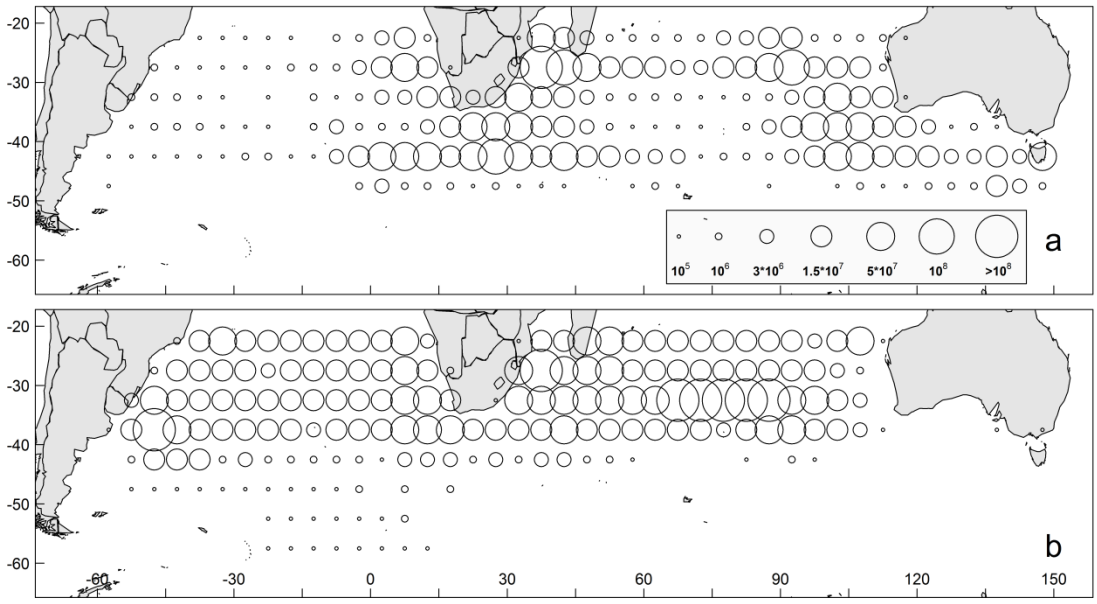

Figure 2.1*. Map of southern Indian and Atlantic Ocean effort by (a) Japanese and (b) Taiwanese fleets, cumulative effort (number of hooks) from 1990 through 2005. See methods for effort calculation.*

The relative availability and value of each target species can vary in space and time, related to species-specific ecology as well as annual quota cycles. Regarding species ecology, each species has a unique distribution, including the timing and location of spawning

(Arrizabalaga et al., 2014; Chen et al., 2005; Farley and Davis, 1998; Frédou et al., 2007). SBT spawning occurs in tropical regions generally in the summer (SCRS 2014), with peak spawning abundance noted in September-October and February-March (Caton, 1991b; Farley and Davis, 1998). Indian Ocean ALB spawning grounds are located across the basin between approximately 10° S - 25° S (Nishida and Tanaka, 2008), while suspected spawning aggregations have been found farther south (20° S – 50° S) in the Atlantic Ocean (Frédou et al., 2007). Spawning tends to occur in spring and summer in both locations. Catch data suggest that BET may spawn in tropical west African waters from approximately 10° N – 10° S in the winter and around 0° - 10° S in the summer, when sea surface temperature is over 25° C (Fonteneau et al., 2004). Migration to the spawning grounds and spawning itself is an energetically demanding process decreasing fat reserves, and therefore value, of tuna meat. Conversely, pre-spawning adults tend to have large fat reserves, creating some of the highest quality meat (Caton, 1991a). For catches regulated by annual quota cycles, the temporal distribution of effort may vary according to how much quota remains. This is suggested to be the case with SBT, where the majority of effort is deployed in the first half of the quota year, which begins in April (Tuck et al., 2003). Given these dynamics, if the magnitude and distribution of effort for each fleet relates to targeting different tunas at different times, it follows that the area fished by each fleet may encompass distinct habitats.

A range of approaches has been used to describe temporal variation and investigate environmental correlates of industrialized distant-water pelagic longline effort. Previous studies of catch or catch per unit effort (CPUE) have applied wavelet and multivariate analyses (Corbineau et al., 2008; Corbineau et al., 2010; Ménard et al., 2007; Rouyer et al., 2008) or generalized additive models (Fonteneau and Richard, 2003; Maury et al., 2001). They have

identified associations of species-specific catch and/or CPUE with climate indices, ocean temperature, and salinity (Corbineau et al., 2008; Corbineau et al., 2010; Lan et al., 2013; Maury et al., 2001; Ménard et al., 2007). Collectively, these studies have shown that environmental variables influence the distribution of fishing effort, and that these patterns vary between oceans and fleets, but a range of issues remain unresolved. For example, the findings from multivariate and wavelet approaches can be difficult to interpret in an ecological or mechanistic context and single species insights may not be applicable to fleets that target more than one species. Furthermore, most studies have focused on equatorial to sub-tropical regions, without extension to the highly fished poleward latitudes.

In this study, we develop the first quantitative analysis of the environmental associations of Japanese and Taiwanese distant-water pelagic longline effort in the southern Indian and Atlantic Oceans. The aims of this study are to identify the environmental variables most associated with fishing effort and suggest potential drivers producing broad-scale patterns in the distribution of effort, considering physical, ecological, and management contexts. Using generalized additive models, we model the magnitude (indicating fishing intensity) and distribution (indicated by the latitudinal gravitational centre) of effort with environmental variables encompassing distinct temporal and spatial scales.

2.3 Methods

2.3.1 Study region

We focused on the Indian and Atlantic Oceans, south of 20° S (Fig. 2.1). This region encompasses broad expanses of open ocean, relatively shallow bathymetric features such as the Kerguelen plateau and the Scotia Arc, and is dominated by meanders of the Antarctic

circumpolar current (Belkin and Gordon, 1996; Stramma and England, 1999). A wide range of important tuna and billfish habitats occur within this region (Arrizabalaga et al., 2014; Reygondeau et al., 2012).

2.3.2 Fisheries data

Longline fishing involves deployment of lines from which hundreds to thousands of hooks are suspended, and is the predominate tuna fishing method in the Southern Ocean. Fishing data from deep-freezing longline vessels were obtained from the Indian Ocean Tuna Commission (IOTC; http://www.iotc.org/English/data/databases.php) and provided by the International Commission for the Conservation of Atlantic Tunas (ICCAT). For the Taiwanese Indian Ocean yearly data, the annual catch data was generally larger than the sum of the monthly logbook catch data. To obtain a more accurate estimate of effort, the number of hooks in the monthly logbook data were raised by the ratio of reported yearly catch to the annual sum of monthly logbook catch (Campbell, 2003). As Japanese data are believed to be the best available, the data were not adjusted (Campbell, 2003; Tuck et al., 2015). Although there are possibly inaccuracies in the reported species catch and/or effort location in the Japanese fleet (Polacheck and Davies, 2008), it was beyond the scope of this study to account for this issue, and, to our knowledge, data accounting for this correction do not exist.

Our analysis was constrained to 1990 through 2005, inclusive; a period of relatively stable management and fishing activity in the Indian and Atlantic Oceans. This temporal restriction was designed to minimize the impact of major changes in management, development, or market-driven changes on fishing effort, which could interact with the relationship of fishing effort with the environmental variables evaluated. We excluded data from the early, more exploratory stages of the fishery; 1950s -1960s, and from the 1970s to mid-1980s, which were

influenced by increased fuel prices, changes in market demand, technological developments and the declarations of Exclusive Economic Zones (Caton and Ward, 1996). Effort declined sharply between 1989 and 1990, likely due to reduced catch limits for SBT (Caton, 1991b; Tuck, 2004; Tuck et al., 2003). A relatively stable 16 years followed, until 2006. The Taiwanese BET quota was then sharply reduced in the Atlantic (Chen, 2012). Fleet capacity for tropical tunas was held at 2006 levels, followed by capacity for swordfish and ALB in 2007 (Moreno and Herrera, 2013). This coincides with a reduction in Japanese pelagic longline effort in the southern Atlantic (Fig. 2.2).

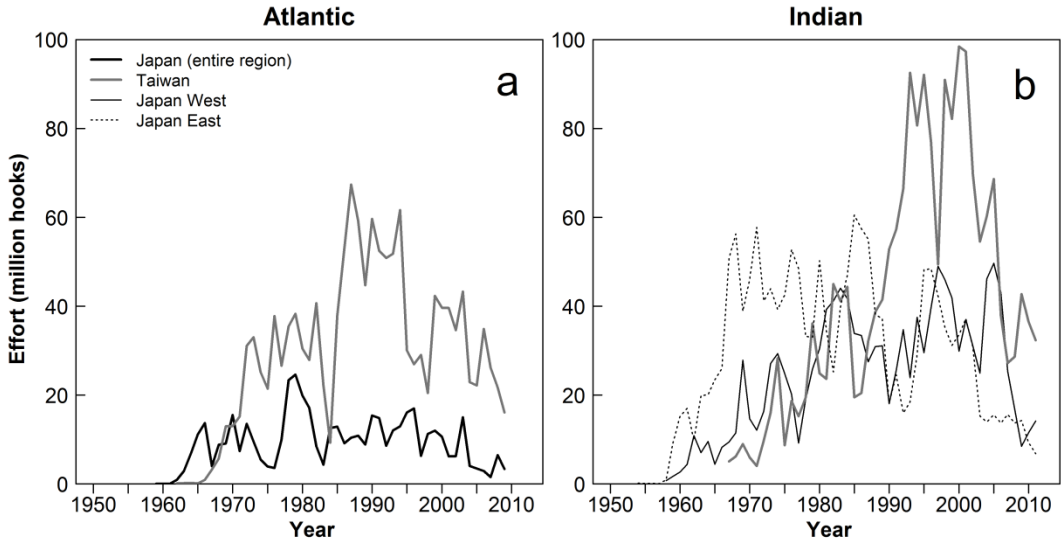

Figure 2.2. *Annual effort in millions of hooks south of 20°S in the (a) Atlantic and (b) Indian Oceans by Japanese and Taiwanese pelagic longline fleets. Japanese effort in the west and east Indian Ocean is plotted separately. Data from 1990 through 2003 and 2004 through 2005 were used in the models and validation, respectively. See methods for effort calculation.*

Despite our attempts to reduce the impacts of non-environment driven changes in the study period, some changes in management did occur during the timeframe evaluated. However, the impacts of these changes were likely restricted to Australian and New Zealand Exclusive

Economic Zones, representing a very small proportion of the southeastern Indian Ocean. Specifically, disputes over global SBT quota allocation resulted in the Japanese withdrawing from a Japanese-Australian joint-venture agreement in the Australian Fishing Zone (AFZ) in 1996 (Campbell et al., 2000). No total allowable catch was set for SBT in 1998 and 1999. At this time, Japan was also excluded from Australian and New Zealand EEZs and unilaterally established an experimental fishing program (Cox et al., 1999; Tuck, 2004).

As Japanese longline effort in the Indian Ocean differs by region, we chose to divide Japanese effort in the Indian Ocean into a west and east component at 70° E, as effort seldom occurs near this longitude and effort in the regions to the west and east tend to occupy different distributions of latitude (Fig. 2.1). The 70° E split also corresponded to the Kerguelen Plateau that influences the movement of currents and hence the location of isotherms, or bands of constant temperature. In the Atlantic, the Scotia Arc (20° W) formed a similar natural boundary between east and west. Time series for the maximum extent of sea ice were also created for the west and east based on this definition and used only in models of Japanese effort in the Indian Ocean (see 'environmental variables' section below for details).

We evaluated two different characteristics of fishing effort: the magnitude and distribution. We assessed the magnitude of fishing effort by summing the number of hooks deployed each month. Though hook setting practices and the amount of time the line is left in the water contribute to the overall dynamics of effort, this information was not available at the time of analysis. While other studies evaluate catch or catch per unit effort (CPUE; Corbineau et al., 2010; Maury et al., 2001; Ménard et al., 2007), our focus is on the total magnitude of regional effort across potentially different target species. Likewise, we did not consider if

changes in effort reflected changes in the number of vessels fishing or a change in the effort of individual vessels.

To track changes in the distribution of fishing effort, the 'latitudinal gravitational centre' (hereafter: distribution) of fishing effort was calculated (Lan et al., 2013; Lehodey et al., 1997). The number of hooks per km^2 was used instead of catch per unit effort, as a target species was not clearly indicated by the data and longline gear configuration information was not provided from which target species could be inferred (but see Satoh and Okamoto (2012) for Indian Ocean Japanese longline CPUE for BET tuna). Due to observed (Booth et al., 2011; Polovina et al., 2008; Worm and Tittensor, 2011) and projected (Hartog et al., 2011; Hobday, 2010; Sunday et al., 2012) shifts in the distribution of pelagic habitats and / or species and catch potential (Cheung et al., 2010), the change in the mean latitude of fishing effort was calculated as:

$$G\ Lat_j = \frac{\sum_i Lat_i * E_{ij}}{\sum_i E_{ij}} \qquad (2.1)$$

where Lat_i is the latitude of the midpoint of the i^{th} latitudinal section and E_{ij} is the number of hooks per square kilometre in the i^{th} latitudinal section at time j.

2.3.3 Environmental variables

All environmental variables were assessed at a monthly temporal scale, from 1990 through 2005, inclusive.

2.3.3.1 Isotherms

Temperature isotherms are frequently associated with the broad-scale structure of tuna fishing (Chen et al., 2005; Hartog et al., 2011; Lan et al., 2013). Given the projected poleward shift of tunas and billfishes (Hobday, 2010), catch potential (Cheung et al., 2010) and likely associated fishing effort, the monthly location (mean latitude) of different SST isotherms was

evaluated. Zonally averaged monthly isotherm locations at 1° C intervals were derived from isotherms 5°C-30°C in the southern hemisphere from the National Centers for Environmental Prediction Reanalysis product (Kalnay et al., 1996) with a spatial resolution of 2.5° in both latitude and longitude (Table 2.1). The data were linearly interpolated to a 0.5° resolution. Following preliminary analysis considering co-variation, a subset of isotherms was selected to represent the range of spatial and temporal variability in the study areas with minimal overlap. West and east isotherms for the Indian Ocean included 5° C, 11° C, 16° C, 22° C, and 27° C while the Atlantic included west and east 5° C, 12° C, 19° C, and 25° C.

***Table 2.1**. Summary of the data sources and ecological interpretation of the habitat variables. All variables were assessed at a monthly scale, from 1999 - 2005, inclusive. Isotherm locations were separated into eastern and western components at 70° E and 20 ° W in the Indian and Atlantic Oceans, respectively.*

Variable	Data source	Interpretation
Zonally averaged isotherm location		
Indian: 5, 11, 16, 22, 27 (°C)	http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.derived.html	Spatially representative fine-scale variation
Atlantic: 5, 12, 19, 25 (°C)	http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.derived.html	Spatially representative fine-scale variation
Sea ice		
Maximum latitude	http://nsidc.org/data/NSIDC-0051	Intermediate-scale regional variation
Climate indices: interannual		
Multivariate ENSO Index	http://www.esrl.noaa.gov/psd/enso/mei/#data	Broad-scale interannual variation
Dipole Mode Index	http://www.jamstec.go.jp/frsgc/research/d1/iod/iod/dipole_mode_index.html	Indian Ocean regional interannual variation
Climate indices: multidecadal		
Pacific Decadal Oscillation	http://jisao.washington.edu/pdo/PDO.latest	Broad-scale zonal low-frequency variation
North Pacific Gyre Oscillation	http://npgo.o3d.org/data/NPGO.txt	Broad-scale meridional low-frequency fluctuation
Atlantic Multidecadal Oscillation	*http://www.esrl.noaa.gov/psd/data/timeseries/AMO/	Atlantic Ocean regional low-frequency variation

*We used the unsmoothed dataset

2.3.3.2 Maximum latitude of sea ice extent

While pelagic longline effort is unlikely to be directly impacted by variation in the extent of Antarctic ice cover, sea ice conditions are used as an indicator of broad scale southern Ocean conditions (Nicol et al., 2000). Sea ice area data were derived from National Snow and Ice Data Center's Sea ice Concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data from 1979-2010 (Cavalieri et al., 1996 ; Table 2.1).

2.3.3.3 Climate indices: interannual variability

To evaluate the potential association of fishing effort with environmental variation occurring on a regional level and on interannual scales, we assessed indices from both ocean basins (Table 2.1). The El Niño Southern Oscillation (ENSO) is associated with the irregular oscillation of sea surface temperature anomalies on interannual timescales in the tropical Pacific (generally 3-4 years; McPhaden, 1999; Zhang et al., 1996). It is considered the globally dominant mode of climate variability at interannual time scales, with significant teleconnections to other basins (Chavez et al., 2011). Both the multivariate ENSO index (MEI; Wolter and Timlin, 1998) and the Southern Oscillation Index quantify ENSO variability. However, we used the MEI because it has a mean of zero, a standard deviation of one and it is calculated from a suite of ocean and atmosphere variables, rather than just the Darwin to Tahiti air pressure gradient. The Dipole Mode Index (DMI) is the gradient of SST anomalies across the western equatorial and southeastern Indian Ocean. This gradient represents the intensity of the Indian Ocean Dipole (IOD; Saji et al., 1999) and has been associated with fishing effort in the Indian Ocean (Corbineau et al., 2008; Lan et al., 2012a; Lan et al., 2012b).

2.3.3.4 Climate indices: multi-decadal oscillations

Lastly, we included climate indices from both basins, which represent multi-decadal oscillations in the environment (Table 2.1). The Pacific Decadal Oscillation (PDO) is the first empirical orthogonal function, EOF1, of the analysis of the detrended sea-surface temperature anomalies north of 20° N in the Pacific (Mantua et al., 1997). Similarly, the North Pacific Gyre Oscillation (NPGO) is the EOF2 of SST and sea-surface height anomalies north of 25° N in the Pacific (Di Lorenzo et al., 2008). Lastly, the Atlantic Multidecadal Oscillation (AMO) is an index of linearly detrended north Atlantic sea surface temperatures (Enfield et al., 2001).

2.3.4 Quantifying associations between environmental variables and fishing effort

Generalized additive models (GAMs) were used to predict the monthly magnitude or distribution of fishing effort using environmental variables as predictors. GAMs enable the identification of non-linear relationships, which have been previously found when associating tuna distribution with the environment (Maury et al., 2001) as well as fishing effort (Davies et al., 2014). Both the magnitude and distribution of fishing effort were each modelled from five datasets; Japanese west and east Indian Ocean, Taiwanese Indian Ocean, Japanese Atlantic, and Taiwanese Atlantic Ocean, for a total of 10 models.

Months with no effort were excluded from the analysis. Due to observed over-dispersion of the fishing effort data, we used the quasi-Poisson distribution in all models. As this quasi-distribution prevents the use of information-theory based model ranking, such as the Akaike Information Criterion, we used a combination of variable significance and the proportion of null deviance explained to identify a parsimonious model. Null deviance explained is likely a better metric of comparison between models than the adjusted R^2 when non-normal errors are likely, as is our case (Wood, 2014). Cubic spline regressions were used with the option to use up to 30

knots (connections between 'sections' of a variable), with more knots indicating a more flexible fit. Smoothing parameter estimation was performed using the REML estimation.

From each of the four variable categories described above, we determined the predictor variable that explained the most variability, and combined these into initial models. The exception to this was the isotherm category, where we included the three most related isotherms. We chose to allow multiple isotherms to be included as each isotherm may reflect regional patterns in effort not associated with a different isotherm. In the case of Japanese effort in the west or east Indian Ocean, only isotherms from the corresponding region were evaluated. Based on expected relationships, the DMI and AMO were only assessed for Indian and Atlantic Ocean models, respectively. When the selected variables were combined into a single GAM, they were arranged in descending order of the percent deviance explained. To reduce the model to contain only important variables, the least significant (highest approximate p value) variable was removed and the remaining variables re-modelled, until only marginally significant ($p < 0.1$) and significant ($p \leq 0.05$) variables remained. As the distribution or magnitude of effort may be related more to a general seasonal cycle than to the environmental variables, we explicitly modelled seasonal variation. We added a simulated seasonal cycle: sine (day of year / 2) in degrees using a cyclic spline as the first term of the model. This produces half of a sine curve per year, with the peak corresponding to late June. Sine and cosine curves are commonly used to simulate seasonal cycles (Hales et al., 2012). We defined seasons as follows: summer (December-February), autumn (March-May), winter (June-August), spring (September-November). To identify the most parsimonious final model, the least significant variable was removed until removing a significant variable reduced the proportion of null deviance explained

by > 5% (Chang et al., 2010). Models were run in R using the mgcv package and custom scripts (R Development Core Team, 2016) using the mgcv package (Wood, 2014) and custom scripts

2.3.5 Model validation

To assess the predictive capabilities of the identified models, we withheld the final two years (2004 through 2005) from the original modeling process. We then used the final model for each fleet-region to predict the magnitude and distribution of effort of the withheld data. Following Chang et al. (2010), we then regressed the predicted magnitude or distribution of effort against the observed magnitude or distribution of effort using a linear regression model:

$$Ef = a + b * Ef'$$

where *Ef* is the observed metric (either the magnitude or distribution) of effort, *Ef'* is the predicted metric of effort, and *a* is a coefficient indicating the systematic bias in (or intercept) in the predicted metric of effort. A coefficient of b which is not significantly different from 1 indicates that the observed and predicted values are similar. This relationship was assessed using a student's t-test.

2.4 Results

2.4.1 Fisheries data

In the 16 years of Japanese and Taiwanese longline fishing evaluated, effort was reported within the study area 97.5% of the time (936 of 960 potential month, year, fleet-region combinations). Effort in the Atlantic Ocean portion of the study area was slightly less frequent than in the Indian Ocean, with 95% and 99% of months with effort observed, respectively. Japanese effort in the Atlantic was the least regular in terms of occurrence, with no effort reported for 19 (5%) months in the time frame evaluated. The location of reported effort ranged

from 20° S in both oceans to 50° S and 60° S in the Indian and Atlantic Oceans, respectively (Fig. 2.1). The total magnitude of effort summed across fleets was much greater in the Indian (2,213 million hooks) than Atlantic Ocean (800 million hooks).

The magnitude and distribution of effort varied by fleet and by region. The magnitude of Taiwanese effort was greater than Japanese by 167.1 million hooks in the Indian (west and east Indian combined) and 455.4 million in the Atlantic Ocean. In the west Indian Ocean, the magnitude of Japanese effort averaged 3.0 million (± 0.2 million SE) hooks per month and was centered on 31.6 °S ±0.4 SE. The magnitude of eastern effort was generally less (2.4 million, ±0.2 million SE), and slightly more poleward at 32.8 °S ± 0.4 SE. Taiwanese Indian Ocean effort averaged 6.2 million (± 0.4 million SE) hooks per month and was centered at 30.8°S ± 0.2 SE. In the Atlantic Ocean, Japanese effort was 1.0 million (± 0.1 million SE) hooks per month and averaged more poleward at 33.3 °S ± 0.4 SE than in the Indian Ocean. Taiwanese effort averaged much higher than Japan at 3.3 million± 0.1 million SE hooks per month and more poleward than Taiwanese effort in the Indian Ocean, with an average latitude of 31.8 °S ± 0.3 in the Atlantic. The magnitude and distribution of monthly effort of all regions and fleets over time are shown in Fig. 2.3.

2.4.2 Environmental variables

Regarding our first aim of identifying the environmental variables most associated with variation in fishing effort, the final models included from one to three variables and explained 30-80% of the variation in effort (Table 2.2). All variable classes were included in one or more models. The seasonal cycle was included in all but one model (east Indian Ocean Japanese distribution of effort) and was the strongest variable in seven of those nine models. Winter related to either the greatest magnitude or most poleward distribution of effort in eight of the

nine models that included seasonal cycle. As the exception to the above relationship, Japanese east Indian Ocean magnitude of effort peaked around April and September (Table 2.2).

Table 2.2. *Monthly, seasonal, and yearly associations with relatively elevated magnitude or poleward distribution of fishing effort indicated by variables included in the final models of Indian and Atlantic Ocean Japanese and Taiwanese effort. This is depicted annually (across an entire row) for climate indices. Dev. Expl. = deviance explained, Season = simulated seasonal cycle, isotherms are referred to by their temperature (°C) followed by W (west) or E (east), Ice = maximum latitude of sea ice extent, # knots = number of knots used in the model, edf = estimated degrees of freedom. Darker shades of grey indicate a stronger relationship with the metric of effort. The order of the variables in the final model reads from top (first) to bottom (last). Dotted lines facilitate seasonal classification of associations.*

Fleet	Ocean: region	Effort	Dev. expl.	Variable	edf	# knots	Months or years associated with elevated or poleward effort for a given variable
							Summer Autumn Winter Spring 12 1 2 3 4 5 6 7 8 9 10 11
Japan	Indian: east	Magnitude	61.4	Season	4	9	
				16C E	3	19	
				MEI	5	30	high or negative: 1996 - 1997
Japan	Indian: east	Distribution	30%	16C E	3	19	
Japan	Indian: west	Magnitude	72%	Season	3	9	
				Ice	1	30	
Japan	Indian: west	Distribution	72%	Season	3	9	
				27C W	7	30	
Taiwan	Indian	Magnitude	80%	Season	3	9	
				22C W	3	27	
Taiwan	Indian	Distribution	61%	Season	3	9	
				Ice	2	30	
				MEI	6	30	low: 1999
Japan	Atlantic	Magnitude	79%	Season	2	9	
				25C W	5	29	
Japan	Atlantic	Distribution	56%	Season	4	9	
				19C E	6	30	
Taiwan	Atlantic	Magnitude	66%	Season	1	9	
				MEI	8	30	weakly positive: 1990, 2003, 2004
				AMO	5	30	negative: 1991-1994
Taiwan	Atlantic	Distribution	44%	Season	1	9	
				25C W	4	30	
				MEI	4	30	moderatly positive: 1991-1994, 2002

The next most important variables related to effort were generally the location of isotherms and the maximum latitude of sea ice extent. While the relationship of effort with

individual isotherms varied by location and season, an elevated magnitude or poleward distribution of effort was correlated with a reduced winter sea ice. The climate indices were ranked second in one of four models, which contained two climate indices, or third (four of four models) in their relationship to effort (percent of deviance explained). These modes highlighted years of anomalous magnitude or distribution of effort which were not associated with the other variables. One exception to this general order importance was the Atlantic Taiwanese magnitude of effort model, which was ordered as follows (in descending order of percent deviance explained): season, MEI and AMO (Table 2.2).

2.4.3 Model validation

Two models did not show a significant bias in model estimates of the distribution of effort nor significantly different values from the observed data. These models were the distribution of Japanese effort in the east Indian Ocean and the distribution of Taiwanese effort in the Indian Ocean (Table 2.3). The distribution of effort in both fleets in the Atlantic Ocean as well as the Japanese fleet in the west Indian Ocean was predicted to occur more poleward than observed (intercept greater than 0, coefficient greater than 1; Fig. 2.3b, h, j). Although the intercept of the Japanese Atlantic magnitude of effort model identified a bias of underestimating the magnitude of effort (significant and positive intercept), effort was greatly over predicted by the model for the validation period (coefficient smaller than 1; Table 2.2, Fig. 2.3g). The magnitude of effort was also over predicted in the Japanese fleet in the east Indian Ocean. The only magnitude of effort model which under predicted effort was in the Japanese west Indian Ocean (coefficient significantly greater than 1; Table 2.3). The magnitude of effort by the Taiwanese fleet was over predicted in both oceans for the validation period (Table 2.3).

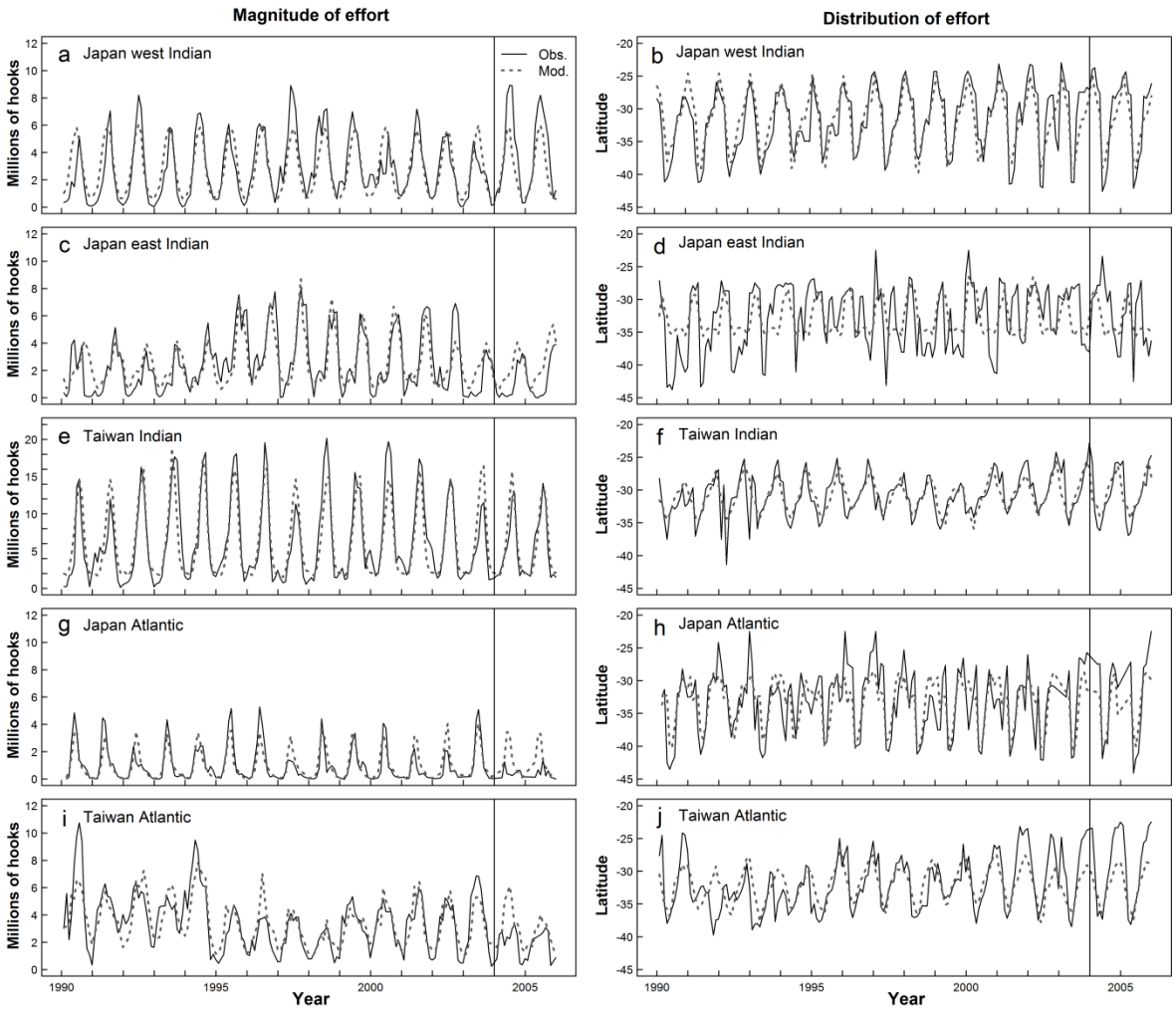

Figure 2.3*. Plots of the observed (solid line) and modelled (dashed line) magnitude (million hooks per month; a, c, e, g, i) and distribution (monthly latitudinal gravitational center; b, d, f, h) of Japanese and Taiwanese pelagic longline fleets in the southern Indian and Atlantic Oceans. Obs. = observed data, Mod. = modelled data. The solid vertical line at 2004 on each plot indicates the beginning of the validation data (2004-2005). Fleet and region are described across rows. Note different scale for ' e'. Months with no effort were excluded from modeling.*

***Table 2.3**. Summary of model validation results of the regression of the observed metric of effort on the predicted for 2004-2005 data. The following equation was applied: $Ef = a + b * Ef'$ where Ef is the observed metric (magnitude or distribution) of effort, Ef' is the predicted metric of effort, and a is an intercept indicating the systematic bias in the predicted metric of effort. A coefficient of b which is not significantly different from 1 indicates that the observed and predicted values are similar. Significant p-values ($p < 0.05$) and the corresponding intercept / coefficient are indicated by **bold**.*

Fleet	Ocean: region	Effort	Intercept (p-value)	Coefficient (p-value)
Japan	Indian: east	Magnitude	-654,679 *(0.06)*	0.79 *(0.09)*
Japan	Indian: east	Distribution	-5.8 *(0.67)*	0.79 *(0.61)*
Japan	Indian: west	Magnitude	142,114 *(0.76)*	**1.41** ***(0.01)***
Japan	Indian: west	Distribution	**13.9** ***(0.00)***	**1.41** ***(0.00)***
Taiwan	Indian	Magnitude	391,488 *(0.46)*	**0.84** ***0.03)***
Taiwan	Indian	Distribution	6.6 *(0.29)*	**1.22** ***(0.03)***
Japan	Atlantic	Magnitude	**378,103** *(0.02)*	**0.05** ***(0.00)***
Japan	Atlantic	Distribution	**18** *(0.01)*	**1.49** ***(0.02)***
Taiwan	Atlantic	Magnitude	664,543 *(0.12)*	**0.41** ***(0.00)***
Taiwan	Atlantic	Distribution	**32.1** *(0.00)*	**1.91** ***(0.00)***

2.5 Discussion

Management of a globally valuable resource such as tunas is particularly challenging, as multiple species are targeted by multiple fleets (Joseph et al., 2010). By progressively removing environmental variables with a weak relationship to effort, we identified shared, as well as fleet and region-specific, environmental associations. Our analysis of the relationships of effort with temporal and environmental variation suggests that the distribution and magnitude of effort are linked not only to the physical environment, but other factors, including spawning timeframes, and changes in access to a target species likely shape the allocation of fishing effort, as described

below. Validation tests suggest that the GAMs predicted the distribution and magnitude of effort relatively well but with some regional biases.

Our findings indicate a hierarchical structure of environmental relationships with fishing effort, which has previously been suggested in single-species analyses (Maury et al., 2001; Rouyer et al., 2008). This hierarchical structure reveals groupings of environmental drivers based on how much variability they explained in the magnitude and distribution of fishing effort for each fleet-region. The seasonal cycle generally explained the greatest amount of variability in the magnitude and distribution of effort, followed by isotherms and the maximum latitude of sea ice extent. Climate indices generally related less to the distribution or magnitude of effort than the variables mentioned above. We interpreted the relationships of isotherm location and the maximum-latitude of sea ice extent by identifying the location of the feature when it was associated with elevated or poleward effort and the months those locations most frequently occurred. We then discuss how both the spatial location and months related to physical, ecological (spawning), and management (start of the quota year) contexts.

In some cases it is not clear if elevated effort is a response to an increased number of tunas, an attempt to compensate for a decrease in the number of tunas, or a change in the composition of tuna species. While we describe the spawning of each tuna species as broad-scale patterns, individuals do vary widely in their movements and distribution (Fonteneau and Hallier, 2014). Many of the associations we link to fishing effort may be circumstantial, coinciding in time and or space but not necessarily driving the observed patterns in effort. With these concessions, we offer hypotheses of potential mechanisms influencing the observed relationships of environmental variables and fishing effort. We describe the region-scale environmental signals that the variables evaluated may capture, offer hypotheses regarding

potential drivers of the observed relationships, and consider the alignment of these relationships with management timeframes.

2.5.1 Season

The simulated seasonal cycle was generally the strongest pattern and suggested heavy targeting of the preferred target species outside of the spawning season. For Japanese vessels in the west Indian and Atlantic Ocean, seasonality is likely related to targeting SBT in the winter, which is outside of the summer spawning season (Farley and Davis, 1998) and near the beginning of the quota year. This timing aligns with earlier observations that the majority of SBT catches occur early in the SBT quota year (Tuck et al., 2003). While SBT are spawning, effort may switch to targeting relatively equatorward BET.

In the east Indian Ocean Japanese magnitude of effort model, the relationship with season was weaker (the third strongest variable). Seasonal-related increases in effort were restricted to April and September, which coincides with the beginning of the SBT quota year and potential targeting of mature, pre-spawning SBT. The only model to exclude the simulated seasonal cycle was the Japanese east Indian Ocean distribution of effort, where the location of an isotherm (16° C east) was the only variable retained in the model (see 'isotherms' subsection).

For the Taiwanese Indian Ocean fleet, high effort occurs in the central southern region (Fig. 2.1), particularly during winter through early spring. As most of this effort is north of 40˚ S, ALB is likely targeted over SBT (Arrizabalaga et al., 2014). A smaller fraction of the fleet also fishes east of South Africa (Fig. 2.1) and targets SBT (Gunn and Farley, 2000). When adult ALB are spawning north of the study area in the spring and summer (Chen et al., 2005), some effort shifts to the west Indian Ocean and the East Atlantic (Gunn and Farley, 2000).

In the Atlantic Ocean, strong concentrations of Taiwanese effort occur southwest of South Africa, and east of Uruguay and Argentina (Fig. 2.1). It is likely that ALB would be the target species, given the latitude (Gunn and Farley, 2000). Effort is reduced and moves equatorward in the spring and summer, which coincides with spawning concentrations of adults occurring outside of the study area (Frédou et al., 2007).

2.5.2 Isotherms

Isotherm location was included in seven of the 10 models. Our assessment of the spatial and temporal association of elevated or poleward effort with these isotherms suggested one of two relationships with effort; target species distribution or the regional impact of variation in the SST structure within important fishing areas.

Beginning with the isotherms that we suggest relate to target species distribution, the 16° C east isotherm: the strongest variable in the east Indian Japanese magnitude of effort model indicated elevated effort occurring from winter through spring, while the isotherm was located relatively equatorward. This time frame overlaps with the beginning of the SBT quota year and suggests targeting of non-breeding SBT.

In the Atlantic Ocean, the elevated magnitude of Japanese effort indicated by the poleward movement of the 25° C west isotherm into the study area in early summer may reflect targeting SBT before the February – March peak in spawner abundance outside of the study area (Caton, 1991b; Farley and Davis, 1998). As the isotherm moves equatorward out of the study area in mid-autumn, increased effort coincides with the beginning of the SBT quota year.

The importance of regional habitat signals captured by isotherms was indicated in all oceans. In the east Indian Ocean, the 16° C east isotherm, as the lone variable retained in the model, captured seasonal variation in the Great Australian Bight corresponding to a poleward

shift in effort targeting SBT. Specifically, the equatorward movement of isotherms through winter coincided with poleward effort likely targeting SBT in the first three quarters of the quota year.

In the west Indian Ocean, the movement of the 27° C west isotherm around Madagascar highlighted poleward effort in late autumn and late spring to early summer. The poleward distribution of effort suggests targeting SBT early in the quota year, corresponding to the late autumn peak, and between spawning periods in late spring to early summer. Furthermore, Madagascar is known for its high diversity of tunas (Reygondeau et al., 2012) and provides important fishing grounds, as suggested by the association with this isotherm.

For the Taiwanese fleet in the Indian Ocean, an equatorward 22° C west isotherm indicated elevated effort from mid-winter through mid-spring associated with the pre-spawning and winter distribution of ALB (Table 2.2). 22° C is within the 15° C-24° C SST range for high catch rates previously observed (Chen et al., 2005).

Lastly, the poleward shift in Taiwanese Atlantic Ocean effort associated with a poleward 19°C east isotherm likely reflects shifts in species distributions just off South Africa, which this isotherm crosses. This region encompasses a relative northern and southern boundary for SBT and BET, respectively, in the southern hemisphere (Arrizabalaga et al., 2014). Autumn effort likely targets SBT while summer poleward effort probably targets BET and non-breeding SBT off of southwestern South Africa.

2.5.3 Maximum latitude of sea ice extent

The maximum latitude of sea ice extent reflects broad-scale shifts in the Southern Ocean environment that may influence tuna spatial ranges and spawning migrations, which could result in fleets changing their target species. Sea ice was the second most important variable in two

Indian Ocean models: Japanese west magnitude of effort and Taiwanese distribution. In the Indian Ocean models, west Japanese magnitude of effort was greatest and Taiwanese effort was most poleward when sea ice was reduced or poleward, from mid-summer through autumn (Table 2.2). Summer and early autumn include the end of both ALB spawning (Chen et al., 2005) and the primary SBT spawning period (Evans et al., 2012; Farley and Davis, 1998), so most mature adults would not be in the Southern Ocean. The west Indian Japanese fleet may then target BET while the Indian Taiwanese fleet may shift towards the southwestern Indian Ocean to target SBT (Gunn and Farley, 2000).

2.5.4 Climate indices: multi-decadal modes

Multi-decadal mode indices identified years with effort which was un-associated with the other variables modelled (Table 2.2). The relatively low AMO values (particularly 1991-94) with elevated Taiwanese effort in the Atlantic Ocean are challenging to interpret. This is due both to a lack of AMO studies encompassing the focal region and the highly dynamic nature of the areas that Atlantic Taiwanese effort is often greatest: southwest of South Africa and east of Uruguay and Argentina (Fig. 2.2). We suggest that slightly low AMO values relate to either increased effort targeting ALB or possibly increased effort to compensate for lower catch rates or smaller individuals, but are unable to differentiate between these two scenarios or if they are exclusive.

Furthermore, the AMO shifted into a positive or 'high' phase in the late 1990s (Enfield et al., 2001), producing approximately the opposite SST patterns in the Atlantic Ocean. Although the regions off of Uruguay and west of South Africa maintained relatively high concentrations of fishing effort, the overall magnitude of Taiwanese effort in the Atlantic Ocean has reduced over time (Fig. 2.3i). The decrease in effort in the Atlantic Ocean may be related to decreased ALB

habitat quality as areas of tuna habitat warmed rapidly (Hobday and Pecl, 2014) or it could be related to a rationalization of fishing resources and a return to focus effort in the Indian Ocean.

Despite their global signatures (Di Lorenzo et al., 2008; Mantua and Hare, 2002), neither PDO nor NPGO were included in a final model (Table 2.2). This could be due to the short time frame of our study in comparison to the long time-scale encompassed with cycles of these indices, or that these Pacific-based indices are not associated with patterns in the distribution and magnitude of fishing effort in the Indian and Atlantic Oceans.

2.5.5 Climate indices: interannual variability

Inclusion of climate indices in best models could be interpreted in terms of anomalous months and years. The MEI highlighted years with unique effort patterns in four models. Both high positive and negative monthly MEI values, occurring through 1996 and 1997, related to elevated effort in the east Indian Ocean. It is possible that Japanese effort targeted different species in these two unique conditions, both of which resulted in an increase in effort. As negative MEI is associated with slightly cooler SSTs in the Indian Ocean (Chavez et al., 2011), increased effort with negative MEI phases may reflect the fleet's response to cool water species, likely SBT, occupying a larger proportion of the study area. During 'extreme' warm conditions suggested by high MEI values, effort may increase as a result of heavier targeting of BET than SBT, as mature SBT are generally in cooler waters (Arrizabalaga et al., 2014). The 1996-1997 effort association with the MEI values suggesting elevated effort also coincides with instability in multi-lateral management of SBT regarding quota limits. This multi-lateral instability resulted in Japanese fleet exclusion from the Australian Fishing Zone (Campbell et al., 2000). However, we did not attempt to differentiate between the impacts of the MEI and quota management on the magnitude of fishing effort.

For Taiwanese Indian Ocean effort, poleward effort associated with low MEI values (cool conditions), particularly in 1999, may reflect Taiwanese targeting of SBT (poleward distribution) during the conditions that favour this species. In fact, 1999 was the year with the largest by weight of SBT for Taiwan in the Indian Ocean according to the Nominal data. Increased Taiwanese Atlantic effort with weakly positive MEI values generally occurring in 1990, 2003 and 2004 may reflect an adjustment to a slightly reduced catchability of the target species. Previous work has shown that positive MEI values, associated with El Niño events, can alter thermocline depth and change the availability of tuna to some fishing gear (Lehodey et al., 2011). To compensate for a slight change in vertical distribution, the fleet may have increased overall effort or altered the gear to fish deeper, although this could not be confirmed in the dataset used, as hook depth or number of hooks per basket were not provided. Poleward Taiwanese Atlantic effort associated with moderately positive MEI values occurring from 1991 – 1994 and 2002 suggest that effort likely followed ALB as they shifted poleward to remain in cooler waters.

Although previous studies have identified relationships with the DMI (Corbineau et al., 2008; Lan et al., 2012a; Lan et al., 2012b), it was not retained in any of our models (Table 2.2). This is not particularly surprising, as our study area did not overlap with the region from which the DMI values are calculated.

2.5.6 Special case: distribution of east Indian Ocean Japanese effort

It was somewhat surprising that environmental variables in the east Indian Ocean were more related to the magnitude of Japanese effort (60% deviance explained) than to the Japanese zonal centre of effort (34% deviance explained; Table 2.2). This suggests that the lack of a strong model fit for the distribution of effort is not due to the east Indian Ocean being poorly

represented by the environmental variables, but that the distribution of effort is weakly associated with them. Nevertheless, identifying potential drivers in the location of effort in this region is important; particularly as the majority of Japanese SBT catch has historically occurred here.

We suggest that the location of fishing effort in this region was highly influenced by changes in fleet behaviour resulting from quota disagreements and exclusion from the AFZ in 1998 (Cox et al., 1999). Specifically, Japanese effort using Australian quota within the AFZ may have impacted the distribution of effort outside of the AFZ. Furthermore, joint-venture vessels occasionally caught SBT fishing Australian quota outside the AFZ to support the real time monitoring of fish stocks (Campbell et al., 2000; Cox et al., 1999). This may have impacted the distribution but not necessarily magnitude of Japanese effort in the southeast Indian Ocean. Indeed, the magnitude of fishing effort from 1996-2000 (Fig 3c) does appear to be relatively more consistent than the distribution of effort (Fig 3d).

2.5.7 Model validation

The two years of data we used to validate our models followed the time period used to develop the models and thus are not an independent dataset. Despite this lack of independence, the validation process identified significant biases within some of the models which were not as clear in our plots of the observed and modelled data (Fig. 2.3). This includes the poleward bias of predictions of the distribution of effort for both fleets in the Atlantic and the Japanese west Indian Ocean, the general tendency to underestimate the magnitude of Japanese effort in the Atlantic Ocean, and the over prediction of the magnitude of effort across the validation period for both fleets in the Atlantic Ocean, Japan in the east Indian Ocean and Taiwan in the Indian Ocean. Interestingly, two of the weakest models, in terms of percent deviance explained; the

distribution of effort for the Japanese east Indian and Taiwanese Indian Ocean fleets, were the least biased in their predictions. The bias of other models, particularly in the Atlantic, to over-predict the magnitude of effort and to predict a more poleward distribution than was observed could relate to an overall reduced magnitude of effort in the Atlantic Ocean (Fig 1b). Overall, validation tests suggested good predictive ability of our models while identifying some regional biases.

2.5.8 Building towards fine-scale modeling of fleet behavior

Improving the ability to effectively manage fisheries, such as distant water tuna fleets, requires an understanding of factors behind patterns in fishing effort across regions, oceans and different flagstates. By interpreting these relationships in physical, ecological, and management contexts, many of the forces producing the observed associations and patterns in effort over time can be elucidated. In this study, we identified multiple shared relationships across ten distinct region-flagstate patterns of effort, indicating some generality. While management timeframes are related and potentially drive some of the variation in effort, species distribution, particularly related to the spawning season, has a very strong impact on how fleets allocate effort. Given current projections for poleward shifts in tuna distribution (Hobday, 2010) and anticipated changes in spawning habitat (Dueri et al., 2014; Lehodey et al., 2013; Lehodey et al., 2010) prudent resource management would include considering the potential responses of fleets to these changes.

Overall, this study strengthens our understanding of broad-scale fishing dynamics by providing the first quantitative description of the environmental associations of distant-water longline effort targeting multiple species in the Southern Ocean. This enhanced understanding will contribute to development of sustainable management approaches for southern tunas in an

environment that is undergoing long-term change (IPCC, 2013). Further development of and improved accuracy in modelling the potential response of fleets to fine-scale changes in tuna distribution or behaviour can be achieved through contributions from multiple stakeholders.

The fleets and the management organizations they report to could provide or require additional information on fishing practices (e.g. targeting information, depths fished). Continued observation and analysis of natural tuna behaviour and distribution throughout their life cycle by independent and industry-associated researchers is also needed. This can be achieved using chemical tracers (Madigan et al., 2013), dart-tagging programs, (Fonteneau and Hallier, 2014), archival (Walli et al., 2009), and pop-up satellite tags (Patterson et al., 2008). Tuna distribution data can then be assessed in concert with fishing data and environmental variables, enabling individual relationships to be identified with greater confidence. These relationships in turn facilitate the development of integrated models of tuna distribution (Dueri et al., 2014; Lehodey et al., 2013; Lehodey et al., 2010) which can then be linked to models assessing fleet behaviour under different scenarios, incorporating the impacts of fishing on population dynamics (Dueri and Maury, 2013).

Comprehensively identifying factors potentially driving fleet dynamics in pelagic longline tuna fleets requires consideration of the physical, ecological, economic, and management contexts in which these decisions are made (Abbott and Haynie, 2012; Dowling et al., 2013; Dowling et al., 2012). Additional studies on multi-species fleets (Poos et al., 2010; Venables et al., 2009), fleet response to management measures (Dowling et al., 2012), and economic factors (Van Putten et al., 2012) would further this field, and provide robust foundations for projecting potential future changes in fishing effort distribution under a changing climate.

2.6 Acknowledgements

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3 Japanese and Taiwanese pelagic longline fleet dynamics and climate change in the southern Indian Ocean: a shared strategy but distinct targeting

3.1 Abstract

Climate change is projected to continue shifting the distribution of marine species, leading to changes in local assemblages and different interactions with human activities. With regard to fisheries, understanding the relationship between fishing fleets, target species catch per unit effort (CPUE) and the environment enhances our ability to anticipate fisher response and is an essential step towards proactive management. Here, we explore the potential impact of climate change on fleet dynamics in the southern Indian Ocean by modeling Japanese and Taiwanese pelagic longline effort (hooks set). We quantify the catch and variability of different target species, the relative value and cost of fishing in different areas, and then develop four effort allocation strategies that incorporate these parameters. Using linear mixed models, we identify fleet-specific effort allocation strategies most related to observed effort and predict the future distribution of effort and tuna catch under climate change for 2063-2068. Results show that while both fleets share a strategy of allocating effort in areas of low uncertainty, they display fleet-specific targeting practices producing different predicted distributions of effort. Future projections suggest that effort of both fleets will decrease due to increased uncertainty in CPUE predictions. Predicted effort is highly concentrated for the Japanese fleet and more diffuse for the Taiwanese fleet. This fleet dynamics approach provides a useful method to explore the impacts of different management strategies for the changing future.

3.2 Introduction

Climate change is already altering the distribution of fish and fisheries catch (Last et al., 2011; Perry et al., 2005; Poloczanska et al., 2014). Research predicts that the distributions and catches of many important fishes will continue to change (Cheung et al., 2010; Dueri et al., 2014; Hobday, 2010; Lehodey et al., 2015). Our understanding of the relationship between catch and the environment is rapidly developing, particularly for high-value tunas (Arrizabalaga et al., 2014; Corbineau et al., 2010; Glaser et al., 2011; Lan et al., 2013). However, fisher response is notoriously difficult to predict (Dowling et al., 2013; Mangel et al., 2015), sometimes resulting in management having unintended consequences (Abbott and Haynie, 2012; Chan et al., 2014; Fulton et al., 2011).

Managing fisheries, including reducing interactions with bycatch species, requires an understanding of how the species and fishers will respond to local and more broad-scale changes in their surrounding environment. This knowledge is particularly useful when it is used to predict species distribution or fisher behavior ahead of time, allowing for proactive instead of reactive management. One type of proactive management is dynamic management of fisheries using projected species distributions, which has been used in to reduce bycatch in the tuna and billfish fishery off south eastern Australia (Hobday and Hartmann, 2006; Hobday et al., 2010), and in the Hawaiian longline fishery (Howell et al., 2008). In the Australian example, bycatch of southern bluefin tuna is reduced by projecting the division between their habitat and that of the main target species (yellowfin tuna), and providing that information to fishers (Hartog et al., 2011). North of Hawaii, projected turtle habitat maps are used to voluntarily reduce interaction with fisheries (Howell et al., 2008).

The efficacy of these and other dynamic management approaches could increase by coupling them with models of fleet behavior; increasing the ability to anticipate how fishers will respond to natural and management changes (Dowling et al., 2012). Studies on the interaction and communication of different vessels within the same fleet (Gilman et al., 2006; Little et al., 2004; Maury and Gascuel, 2001) have developed an understanding of internal fleet dynamics. Some fleet models are based on a Bayesian approach (Ives and Scandol, 2013), while in other cases object-oriented programming has been used to assess the bioeconomic sustainability of fleets under different policy options (Pelletier et al., 2009). Dynamic state variable modeling has also been applied to explicitly model the fisher decision making process (Dowling et al., 2013; Dowling et al., 2012), including discarding in trawl fisheries (Gillis et al., 1995; Poos et al., 2010).

Distant-water pelagic longlining is the most common method for capturing high-value sashimi-grade tunas (Hamilton et al., 2011) and has an increasing presence in the fleet-dynamics literature (Dowling et al., 2012; Mangel et al., 2015; Pascoe et al., 2013). However, most modeling approaches require a detailed understanding of the economics of vessels (Dowling et al., 2012) or high-resolution (shot by shot) effort data (Mangel et al., 2015; Pascoe et al., 2013). This places a serious constraint on the application of these methods to high-seas longline fisheries, where detailed economics and shot by shot effort date are generally unavailable. The limitation imposed by existing methods suggests a need for an alternative approach when data are limiting or detailed predictions are less essential.

The aim of this study is to explore the impacts of climate change on the distribution of two tuna-targeting pelagic longline fleets. Using the Japanese and Taiwanese fleets in the southern Indian Ocean as a study case, we define fisheries parameters and use them to develop

effort allocation strategies for each fleet. Using fleet-specific linear mixed models specifying a species-specific relationship for each strategy, we then project the distribution of tuna CPUE using environmental parameters that incorporate projected climate change, to predict how each fleet will respond given their fleet-specific effort allocation strategy. Our approach offers multiple stakeholders a way to jointly explore and develop an understanding of fleet dynamics, the impacts of climate change, and the potential to adaptively manage high-seas fisheries.

3.3 Methods

3.3.1 Fishing fleets and study area

To assess the fleet dynamics of longline effort targeting high-value tunas and the subsequent impacts of climate change, we focus on the southern Indian Ocean, 20° S to 50° S (Fig. 3.1). We focus on the Japanese and Taiwanese deep-freezing pelagic longline fleets, as they have a well-established fishing presence on the high seas (Moreno and Herrera, 2013; Tuck et al., 2003). Both fleets target tunas, including tropical to sub-tropical yellowfin, YFT and bigeye, BET and sub-tropical to temperate albacore, ALB and southern bluefin, SBT (Arrizabalaga et al., 2014; Moreno and Herrera, 2013; Reygondeau et al., 2012). The tuna vessels operating in these fleets often remain at sea for 18 months to two years and use carrier vessels to transfer and transport high value catch at sea while the fishers remain close to the fishing grounds (Hamilton et al., 2011). Around 40% of catch is transshipped (Moreno and Herrera, 2013).

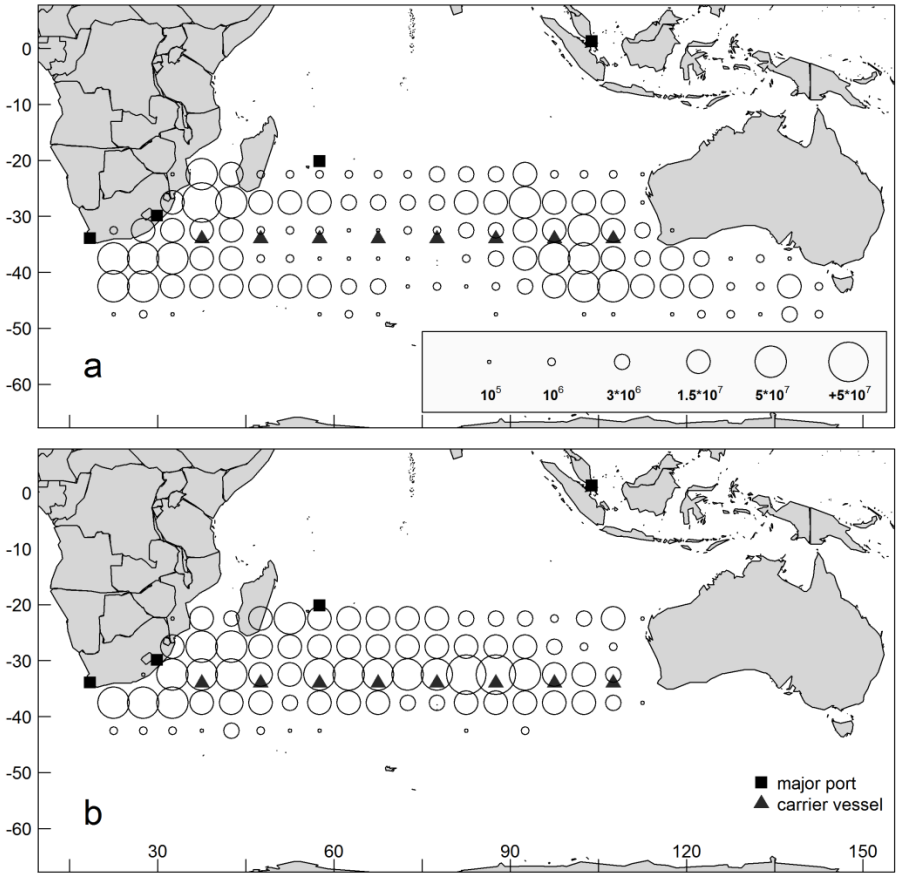

Figure 3.1 *Distribution and magnitude (cumulative number of hooks) of effort for (a) Japanese and (b) Taiwanese pelagic longline fleets, 1998 through 2011. The locations of (black squares) major ports are shown, as well as the approximate location of (grey triangles) carrier vessels derived from Regional Observer Program contractor reports (MRAG and CapFish, 2013, 2015, 2016).*

3.3.2 Data

3.3.2.1 Fisheries data

Fishing catch and effort logbook data from longline vessels were obtained from the Indian Ocean Tuna Commission (IOTC; http://www.iotc.org/English/data/databases.php). These data are at a monthly, 5° latitude by 5° longitude scale. Effort data were standardized (Campbell, 2003; Tuck et al., 2003). Taiwanese catch data were converted to maintain the reported catch

per unit effort and Japanese catch monthly catch data were converted from number to weight (see Appendix A.1 for details). While it would have been ideal to predict the distribution of each species from fisheries independent data, extensive distribution data are not available for each of the species within this study region. To our knowledge, most models of tuna distribution do rely on fisheries dependent data (Dowling et al., 2012; Pascoe et al., 2013) but are not currently available for all of the focal species or within our study region.

3.3.2.2 Environmental data

To characterize the ocean environment and how it relates to species-specific CPUE, we used four environmental parameters: sea surface temperature (SST), sea surface height anomaly (SSHa), chlorophyll (Chl) and bathymetry. These parameters are considered important drivers of fish distribution and often used in models of tuna catch in longline fisheries (Dell et al., 2011; Syamsuddin et al., 2013) and fleet dynamics (Davies et al., 2014). We calculated the arithmetic mean and variance of each environmental parameter at a 5°× 5° longitude by latitude, monthly cell to match the scale of the fisheries data. While this resolution prevents an assessment of mesoscale features which can be associated with tuna catch (Dell et al., 2011), it provides a general indication of the habitat associated with species-specific CPUE. Aggregating to this scale also avoids making assumptions regarding the distribution of fishing effort within a cell, as opposed to downscaling effort to match the environmental data.

SST data were the NOAA ¼° monthly optimum interpolation dataset (Reynolds et al., 2008), with many studies showing the importance of SST in tuna distribution. SSH data were the monthly mean of the AVISO delayed time ¼° monthly mean sea level anomalies computed with respect to a twenty-year mean produced by Ssalto / Duacs and distributed by AVISO with support from the Centre National d'Etudes Spatiales (http://www.aviso.altimetry.fr/duacs/).

These data indicate the relative strength of physical processes, such as upwelling or downwelling, the presence of fronts and eddy activity, which in turn can influence prey aggregation and ocean productivity (Hobday and Hartog, 2014), albeit averaged over a broad spatial scale. Chlorophyll data served as an indicator of primary productivity. We used both monthly SeaWiFS (January 1998 – June 2006) and MODIS (July 2006 – December 2011) products, at $^{1}/_{12}°$ degree resolution. As an evaluation of our model using each dataset identified a similar relationship, we did not create a blended product for the period these products overlapped. To evaluate the possible influence of bathymetry on fleet dynamics, we used data from the GEBCO_08 30 arc-second bathymetric grid (htpp://www.gebco.net).

To forecast the impacts of climate change, we used the BLUElink model (Oke et al., 2008). Climate change forecast data are generated by the Ocean Eddy-resolving Model (Matear et al., 2013; Sun et al., 2012) within BLUElink, based on corrected output from the CSIRO Mk.3.5 output which is forced by the A1B scenario for the 2060s (Hartog et al., 2011). We extracted monthly SST, SSHa, and phytoplankton data for a simulated period 2063-2068, which has been previously used in fisheries assessments (Dell et al., 2015; Hartog et al., 2011). As these data were produced on an irregular grid, data were aggregated to 1° cells before calculating the mean and variance at the 5°× 5° scale. To convert phytoplankton data to Chl values, we multiplied phytoplankton values by 1.59. This conversion factor assumes 50 mg Carbon to 1 mg Chl (Eppley et al., 1998; Sharp et al., 1980). BLUElink data were accessed through the CSIRO data server SDODE (Hartog and Hobday, 2011). SST, SSHa, chlorophyll *a* and bathymetric data were accessed with R using the raadtools package; https://github.com/AustralianAntarcticDivision/raadtools).

3.3.3 Fleet dynamics modeling approach

We used a mixed effects generalized linear model to estimate the relationship between our modelled characteristics and observed magnitude of effort in each cell. We assumed effort was allocated by each fleet according to one of four effort allocation strategies: a balance of value and cost, maximum value, balance of value and variability, or minimum variability (Section 3.3.5). To model these strategies, we first had to develop fishery variables (Section 3.3.4). After identifying the strategy most related to the observed effort in each fleet, we modelled the impacts of climate change on the catch and variability of different fishing areas and predicted the distribution of effort, based on the identified effort allocation strategies (Section 3.3.6). This approach is summarized in Fig. 3.2.

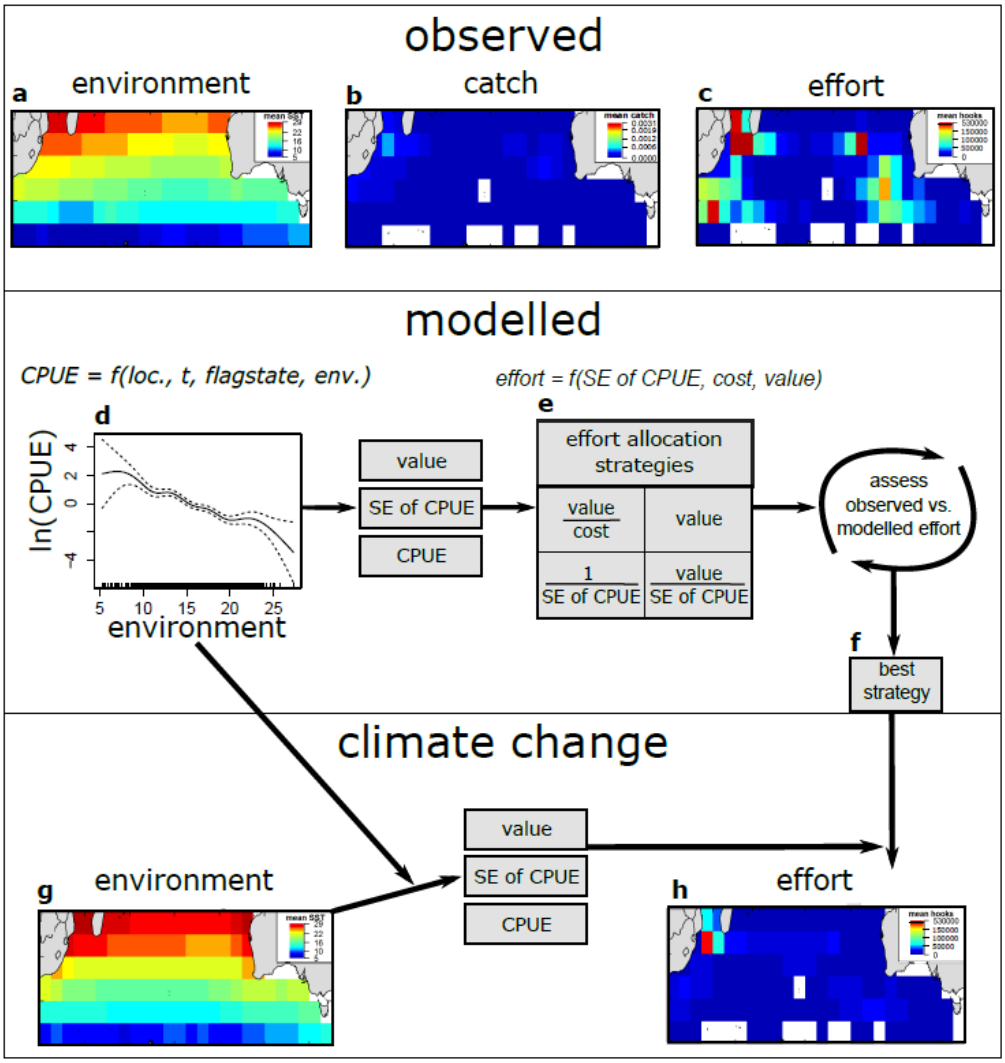

Figure 3.2 *Schematic representation of the approach used to model and project the distribution of fishing effort given climate change (see methods for details). Observed (a) environment (b) catch and (c) effort data were obtained from various online sources. The mean and variance (var.) of the catch per unit effort (CPUE) of major target species was modelled as a function of location (loc), time (t), flagstate (Japan or Taiwan) and the environment (env). This defined a relationship with the environment and allowed the calculation of the value (CPUE mean * species-specific value) of different fishing areas. We then modelled fishing effort based on (e) four different effort allocation strategies, combining different modelled parameters and the cost of fishing in different areas. By assessing the agreement between the (c) observed and modelled effort, the modelled producing the effort most similar to the observed was identified as the (f) historic effort allocation strategy. The impacts of climate change on effort are projected by incorporating environmental data from (g) climate change's impact on the environment into the previously modelled (d) CPUE relationship, producing new CPUE means, SE of CPUE, and values for fishing in a given area. This updated values were applied to (f) the best effort allocation strategy, producing (h) the projected distribution of fishing effort given climate change.*

3.3.4 Fishery variables

We quantified four fisheries characteristics: (i) the area (by longitude, latitude) associated with species-specific catch per unit effort (hereafter: CPUE) of the four focal tuna species, (ii) the standard error of modelled CPUE (hereafter: SE of CPUE), (iii) the value of each tuna species, and (iv) the relative cost of fishing in a given area, defined as the minimum distance from a major port or carrier vessel location.

3.3.4.1 i) CPUE

As the distribution of tunas accessible to fishing gear is an important component to consider when modeling fleet dynamics, we modelled the CPUE of the four focal tuna species. We use a spatial smooth which created a two-dimensional surface across the study area with a factor incorporating fleet and year. After a preliminary assessment of Poisson, lognormal, Gaussian, and Gamma distributions, a lognormal distribution was identified as the most suitable. This created a species-specific spatial surface for each year and fleet. To incorporate environmental effects on the spatial and temporal distribution of CPUE, we used the following equation 3.1:

$$ln(weight / hook) = s(longitude * latitude, by = year\_fleet) + env.\ 1 + s(env.\ 2) \quad (3.1)$$

where '*s*' indicates a thin plate spline smooth, '*year_fleet'* is a factor parameter allowing a unique spatial surface for each year and fleet combination, and '*env. 1'*, '*env. 2'* are environmental parameters. While environmental parameters are correlated with space, the spatial smooth provides greater flexibility in the definition of the relationship of CPUE with a given parameter, allowing it to change across space. We selected the environmental parameters with the two smallest Akaike Information Criterion (AIC) values when modelled one at a time and included them in the model, in order of increasing AIC. Equation 3.1 was used to model the

distribution of species-specific CPUE for each fleet, in cells with previously observed effort from January 1998 – December 2011. This included cells where only a subset of the focal species were caught, meaning that the CPUE of a given species could be modelled in cells where it was not observed. As effort near the southern Australia coastline was infrequently observed for these fleets, this region was excluded from the modelled data.

3.3.4.2 ii) Inverse SE of CPUE

To evaluate the uncertainty in the modelled CPUE for a given cell, we calculated the SE of CPUE estimates for each species. The SE is a result of the spread of observations around the predicted value for a particular combination of parameters. More variability in a particular combination of parameters (e.g. location, time, SST and SSHa) leads to larger SEs. The SE also captures the observation error, so fewer observations at a particular combination will lead to a higher SE, as there is less information with which to estimate the relevant parameter values. We converted this to the inverse SE, where high inverse SE indicates low variability. Both the CPUE and SE of CPUE were retrieved through the predict.gam() function from the mgcv package (Wood, 2014) and were back-transformed.

3.3.4.3 iii) Species-specific value

Price data are needed in order to define the value of each fishing area. The total weight (metric tonnes) and total value (¥) for each tuna species from 2005 through 2011 were obtained from three statistical yearbooks retrieved from the Japanese Ministry of Agriculture, Forestry and Fisheries (MAFF; http://www.maff.go.jp/e/index.html). Given the large storage capacity of the vessels, the rarity of their returning to port (Hamilton et al., 2011) as well as relatively little interannual variation in annual price (Fig. A.9), we assumed the relative value of each species was approximately the average value of each species from 2005-2011. The value of a given

species in a particular time and cell is calculated by multiplying the average price of that species by the CPUE of that species (¥ per hook). Although we have used observed price data, our intent is to identify areas of relatively high or low value as a component influencing fleet dynamics, and not to model the actual value of fishing locations.

3.3.4.4 iv) Cost

The costs of fishing are known to impact fisher behavior and therefore fleet dynamics (Dowling et al., 2012; Haynie and Pfeiffer, 2012; Pascoe et al., 2013; Van Putten et al., 2012). A major cost for these fleets is fuel (Hamilton et al., 2011), which is needed to access fishing grounds, maintain vessel function, and access facilities to offload / transfer their catch. As we lack information on the movements of individual vessels and maintenance costs, we considered the fuel required to access to offloading / transfer facilities as a proxy for cost. Catch can be off-loaded at ports or at-sea using carrier vessels (Hamilton et al., 2011). The major ports include: Cape Town, South Africa (33.9° S, 18.4° E), Durban, South Africa (29.9° S, 31.0° E), Port Louis, Mauritius (20.2° S, 57.5° E), and Singapore (1.3° N, 103.8° E) (Hamilton et al., 2011; Moreno and Herrera, 2013). As we were unable to obtain data on the distribution of carrier vessels in time and space, their locations were estimated from yearly maps from the Regional Observer Program (MRAG and CapFish, 2013, 2015, 2016) of carrier vessel locations and assumed their location is static (see Appendix A.2 for details). Distance was measured in kilometers from the center of each 5°×5° cell using the Great Circle Distance in the spDist function in the 'sp' package of the R statistical language (Pebesma and Bivand, 2005). When not used in a model, costs can be assumed to be constant. Environmental parameters and fisheries characteristics are summarized in Table 3.1.

Table 3.1 *Summary of the environmental parameters and fisheries characteristics evaluated, their source and interpretation. "MAFF" = Japanese Ministry of Agriculture, Forestry and Fisheries, "ROP" = Regional Observer Program. The native scale of each dataset is indicted in "( )" when not a part of the dataset name. All data were aggregated to a monthly, 5° latitude by 5° longitude scale to agree with fisheries data. Modelled fisheries characteristics (species-specific catch per unit effort and standard error) were developed using Generalized Additive Models (see i) CPUE).*

variable category	variable name	data source		interpretation of variable
		observed	climate change	
environment	SST	NOAA ¼° monthly optimum interpolation	BLUElink (monthly, irregular)	proxy for water mass
environment	SSHa	AVISO delayed time sea level anomaly (monthly, ¼°)	BLUElink (monthly, irregular)	relative strength of up/down-welling impacting; watermass, prey aggregation, productivity
environment	Chl	SeaWiFS(1998-01 - 2002-06); MODIS (2002-07 – 2011-12) (monthly, $^{1}/_{12}$°)	BLUElink (monthly, irregular)	an indicator of primary productivity
environment	Bathy	GEBCO_08 30 arc-second grid	same	topographic constraint/association
fisheries characteristic	CPUE	IOTC (monthly, 5°)	see Methods	species and fleet-specific distribution of CPUE as it relates to space, time, and the enviornmet created with GAMs
fisheries characteristic	SE	see Methods	see Methods	variability of CPUE and relative confidence in CPUE GAMs
fisheries characteristic	value	MAFF	same	relative financial value/kg of species-specific catch
fisheries characteristic	cost	Herrera & Moreno (2013), Hamilton (2011), ROP;*	same	relative financial cost of fishing

*locations approximated from (MRAG and CapFish, 2013, 2015, 2016)

3.3.5 Effort allocation strategy development and assessment

To identify how these fisheries characteristics relate to the distribution of effort in each fleet, we assessed the relationship of observed effort with each of four effort allocation strategies. Each strategy emphasizes different characteristics influencing the choice of fishing location and was assessed for each fleet. These four strategies (detailed in Table 3.2) assume that effort is distributed relative to:

1) balance value/cost: fishers allocate effort to areas where the value is relatively high and the cost is relatively low

2) maximum value: fishers fish in areas with high value

3) balance value/variability: effort is allocated to areas of high value and low variability

4) minimum variability: effort is allocated to areas of low variability only

Table 3.2 *Description of effort allocation strategies assessed for Japanese and Taiwanese pelagic longline effort in the southern Indian Ocean. 'no.' is the reference number for a given strategy described above, 'i' is a given species, value = species-specific CPUE * species-specific mean value (Section 2.5), SE = standard error.*

no.	strategy	effort will occur in areas (of)…	parameters used	equation
1	balance value and cost	close to port and of high value	CPUE, value, cost	$\frac{value_i}{cost_i}$
2	maximum value	high value	CPUE, value	$value_i$
3	balance value and variability	high value and low variability	CPUE, inverse SE	$\frac{value_i}{SE_i}$
4	minimum variability	low variability	inverse SE	$\frac{1}{SE_i}$

To predict the fleet-specific distribution and magnitude of effort from these strategies, we used linear mixed models using a lognormal distribution. The fixed effects of the model included the species-specific value for a given effort allocation strategy. This produced a species-specific coefficient, indicating the intensity of targeting a given species within a fleet and the operational differences between fleets due to targeting preferences, or the 'métier' (Ulrich et al., 2012). As we assume that fishers have a short-term memory or affinity for a particular cell, we include a random effect for each cell, allowing effort to shift over time. This is modelled using the following general equation;

$$ln(effort) = f(ALB) + f(SBT) + f(YFT) + f(BET) + (1|factor(cell\_id)) \quad (3.2)$$

where '*f*' indicates an effort allocation strategy equation in Table 3.2, '*cell_id*' indicates a unique identify for each cell and '*(1|factor(cell_id))*' creates a random effect for each '*cell_id*'. To enable direct comparison of species-specific coefficients, each model assumed all species are fished with the same strategy. The best effort allocation strategy model was selected using the AIC. To evaluate the predictive performance of the model, we assessed the correlation of the mean effort for each cell.

3.3.6 Climate change predictions

To assess how fleets may respond to climate change assuming they maintain the strategy most associated with their current distribution and magnitude of effort we predicted the species-specific CPUE using forecast model data from the BLUElink model described above. We incorporated the entire range of observed spatial distributions in CPUE in the predictions by projecting the CPUE and inverse SE of each of the projected years (2063-2068) using the species-specific spatial surfaces from all modelled years (1998-2011). We then calculated the mean CPUE and inverse SE for each projected year. Assuming the strategy determined above, we used these predictions to calculate the effort allocated to each cell. All analyses were carried out in R version 3.1.1 (R Development Core Team, 2016). GAMs were assessed using the mgcv package (Wood, 2014) and mixed effects models using the lme4 package (Bates, 2010).

3.4 Results

3.4.1 Observed effort and environmental parameters

Japanese fishing effort was distributed in two distinct sections; west and east Indian Ocean while Taiwanese effort was relatively uniform across longitudes (Fig. 3.1). No Taiwanese effort occurred south of Australia during our study period. The predicted impacts of climate

change in the southern Indian Ocean SST, SSHa and Chl, include a general increase in the mean SST, with the greatest increase in the east of the study area, but a slight cooling in the central west (Fig. 3.3a-c). SSHa decreases from east to west across the study area (Fig. 3.3d-f) and Chl generally increases, particularly in the southern portions of the study area.

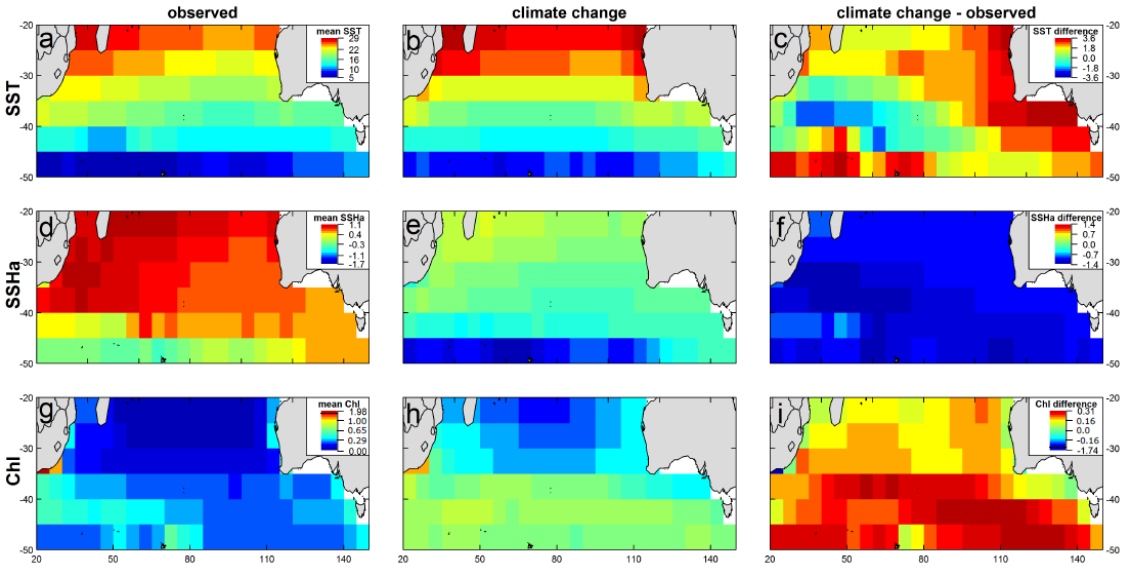

Figure 3.3 *Mean (a, d, g) satellite-based (observed) environmental data from 1998 through 2011, (b, e, h ;) BLUElink modelled under A1B for 2063 through 2068 (climate change), and (c, f, i) difference in the mean value of a cell given climate change minus the mean observed value (climate change – observed). All data are aggregated to the scale of the analysis; monthly, 5° x 5° longitude by latitude. Color scales are the same for observed and climate change plots for a given parameter. Note broken scale indicated by the black line through the colorbar for Chl (g) and Chl difference (i).*

3.4.2 Fisheries parameters

The best CPUE models for each species explained 54.4 to 64.6% of the deviance in the observed data (Table 3.3). SST and SSHa were the strongest and second strongest parameters in three of the four species modelled, respectively. Variance in bathymetry was the strongest parameter in the YFT model, and Chl was the second strongest for the BET model.

Table 3.3. *Summary of species-specific CPUE models of effort across the southern Indian Ocean based off of Japanese and Taiwanese pelagic longline catch data. "env." = environmental parameter, with 1 (2) indicating the first (second) included in the model, "% dev. expl." = percent deviance explained by the CPUE model including both environmental parameters. "var. of bathy." = variance in bathymetry.*

species	env. 1	env. 2	% dev. expl.
ALB	SST	SSHa	59.1%
SBT	SST	SSHa	54.4%
YFT	var. of bathy.	SSHa	64.6%
BET	SST	Chl	53.8%

To understand how each tuna species related to the selected important environmental parameters, we assess the smooths produced by the GAMs used to model the CPUE of each tuna species. The fitted smooth curves suggest that ALB CPUE decreases below 17° C, with a limited effect of warmer temperatures and a moderately positive effect of SSHa above 0.5 (Fig. 3.4a, b). The CPUE of SBT is highest at temperatures below 16° C and SSHa > 0.75 m (Fig. 3.4c, d). While the relationship of YFT CPUE to variance in bathymetry is unclear and sensitive to extreme values, low YFT CPUE is associated with moderate SSHa (Fig. 3.4e, f). Lastly, BET CPUE is highest below 15° C and slightly elevated at temperatures in the mid-20s, but the association with Chl is difficult to discern (Fig. 3.4g, h).

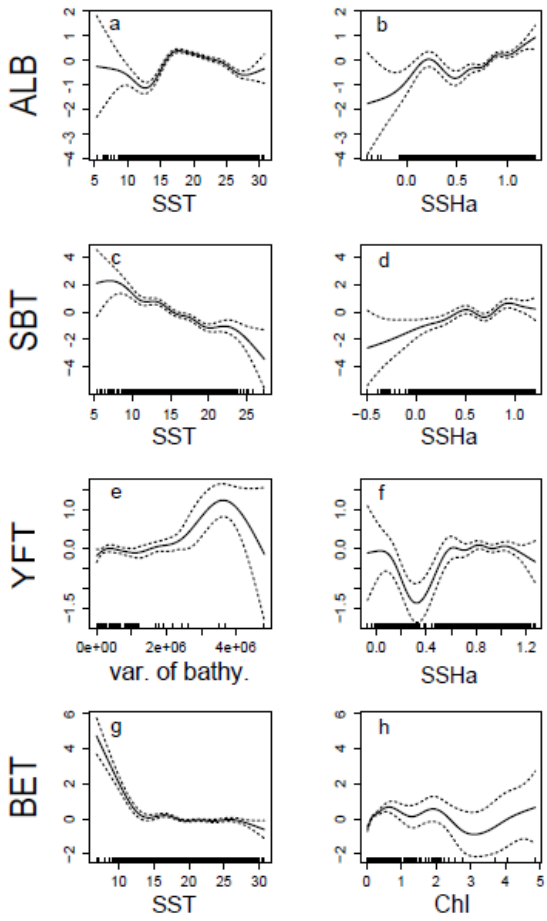

Figure 3.4 *Response of species-specific ln(CPUE) to the environmental parameters in each CPUE model. The frequency of black vertical lines on the x-axis indicates the intensity of observations across values. See Table 3.3 for summary of GAM results.*

The mean cross-species sum of modelled CPUE tended to be slightly higher than observed, with cells near the edges of fished regions, such as the south-central study area for Japan, modelled much higher than observed (Fig. 3.5a, c). Similarly, Taiwanese modelled mean total CPUE was much larger than observed in the eastern edge of the study area (Fig. 3.5b, d). Modelled species-specific CPUE tended to be higher than observed along the edges of the fished region (Fig. A.1-A.4), particularly along the longitudes 50-60° E for SBT (Fig. A.2). For both fleets, predictions with climate change suggest a decrease in the mean cross-species sum of

CPUE compared to the modelled (Fig. 3.5e, f). The mean CPUE of ALB, SBT, and YFT was predicted to decrease with climate change while BET CPUE was predicted to increase (Fig. A.1-A.4). The decreased CPUEs coincided with a large decreased inverse standard error while the inverse SE of BET CPUE only slightly decreased (Fig. A.5-A.8). Areas of high inverse standard error occurred in the west and east for the Japanese fleet and across the central and western portion of the study area for Taiwan (Fig. 3.6a-d). These areas were broader and the values were larger in the modelled than the observed data. Both the spatial extent and magnitude of the mean inverse SE is predicted to decrease in the predictions with climate change, indicating an overall increase in the variability of CPUE (Fig. 3.6e, f).

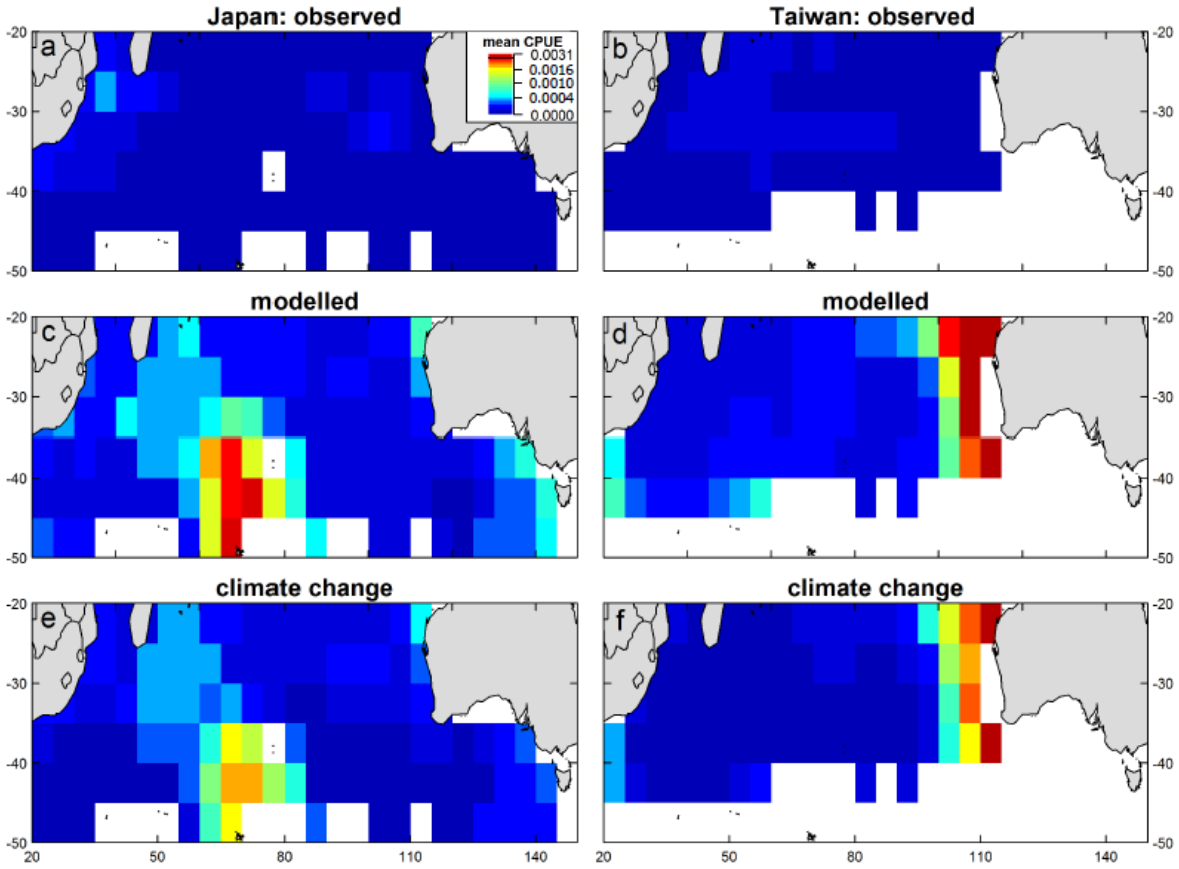

Figure 3.5 *Mean of the cross-species sum of the (a, b) observed, (c, d) modelled, and (e, f) predicted with climate change CPUEs of four tuna species for the (a, c, e) Japanese and (b, d, f) Taiwanese pelagic longline fleets. The CPUE of each species was modelled using a GAM including a spatial smooth and environmental parameters. See Table 3.3 for summary of GAM results. Dark blue indicates very low mean CPUE. Note broken scale indicated by the black line through the colorbar. See Fig. A.1-A.4 for species-specific CPUE plots.*

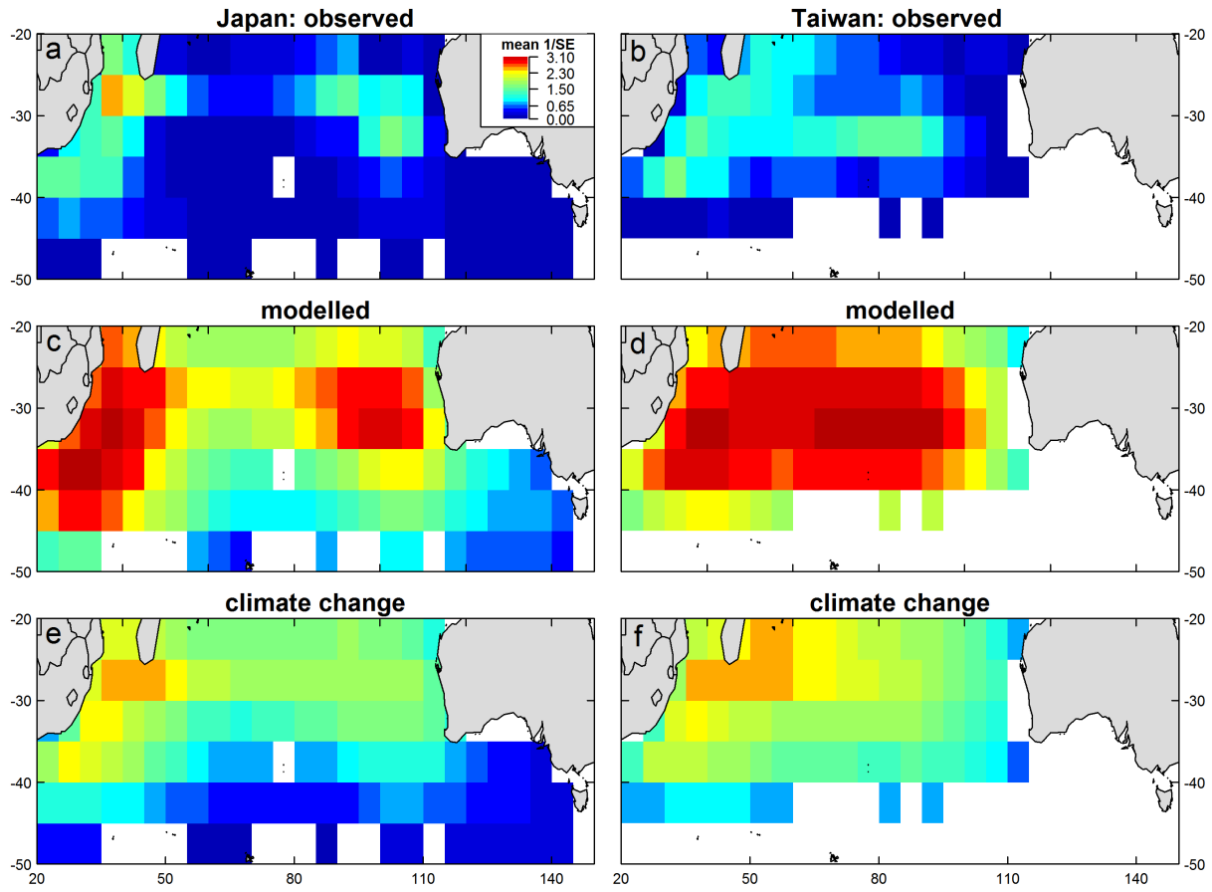

Figure 3.6 *Mean sum of the inverse standard error (1/SE) across species for (a, b) observed, (c, d) modelled and (e-f) predicted with climate change, for (a, c, e) Japanese and (b, d, f) Taiwanese pelagic longline fleets. Dark blue indicates very low mean CPUE. SE values were retrieved from species-specific GAMs modeling CPUE, incorporating both the relative confidence in predictions and the observed variation in CPUE values at a given location / time. See Fig. A.5-A.8 for species-specific inverse SE of CPUE plots.*

The modelled cross-species sum of value was much higher, showing weak agreement(Fig. 3.7a-d). Part of this disagreement is likley relates to our assumption of a static price. The highest value areas occured across the central and particularly south-central study area for the Japanese fleet, and the eastern region for the Taiwanese fleet (Fig. 3.7c, d). Predictions with climate change suggest an overall decrease in the mean value of of tuna catch across the study area when compared to the modelled data (Fig. 3.7c-f). Regarding the cost of fishing, the lowest relative costs occur near ports and approximated carrier vessel locations (i.e.

34° S) while the highest costs occur in the southeast of the study area, south of Australia (Fig. 3.8) where no carrier vessel was allocated (Fig. 3.1).

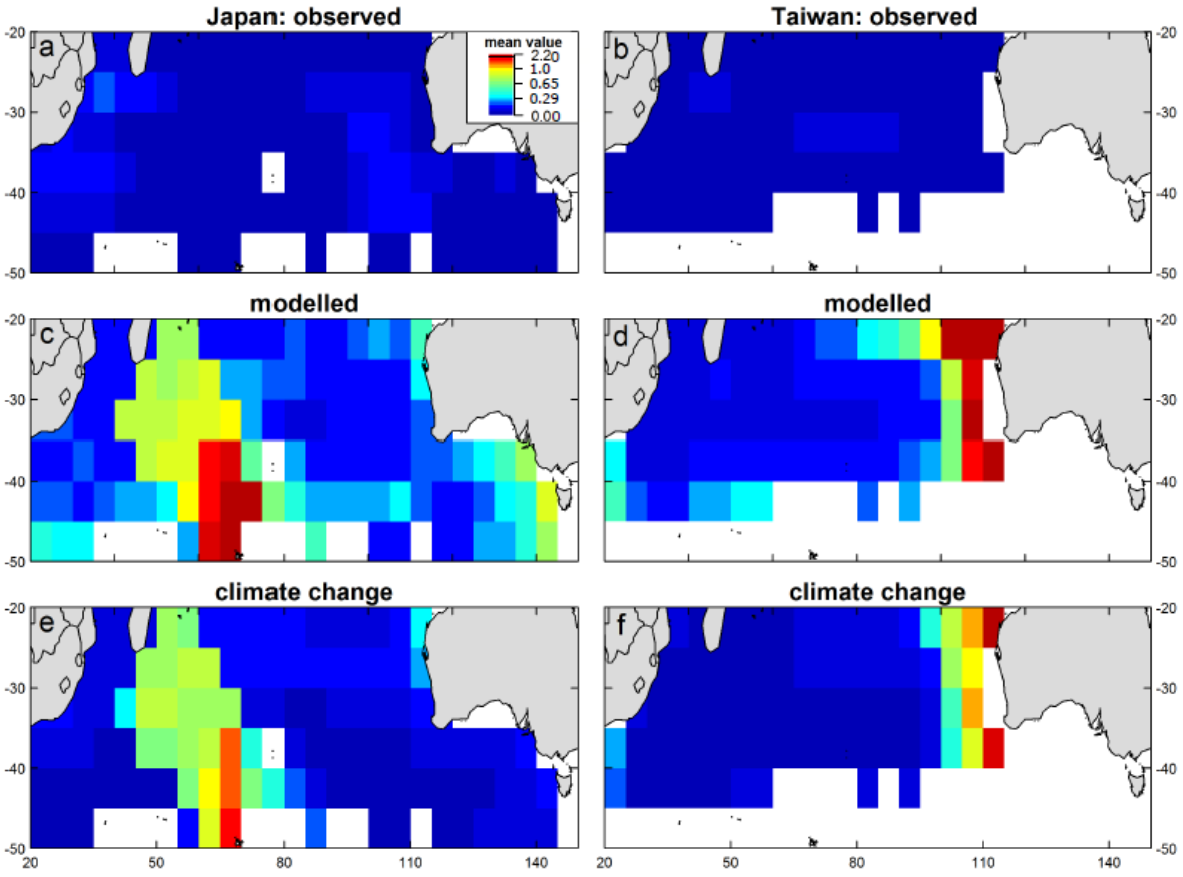

Figure 3.7 *Mean of the sum of the relative value across species for (a) observed, (b) modelled and (c) predicted with climate change data, for the Japanese fleet. The relative value of each species is assumed to remain constant. Dark blue indicates very low mean CPUE. Note broken scale indicated by the black line through the colorbar.*

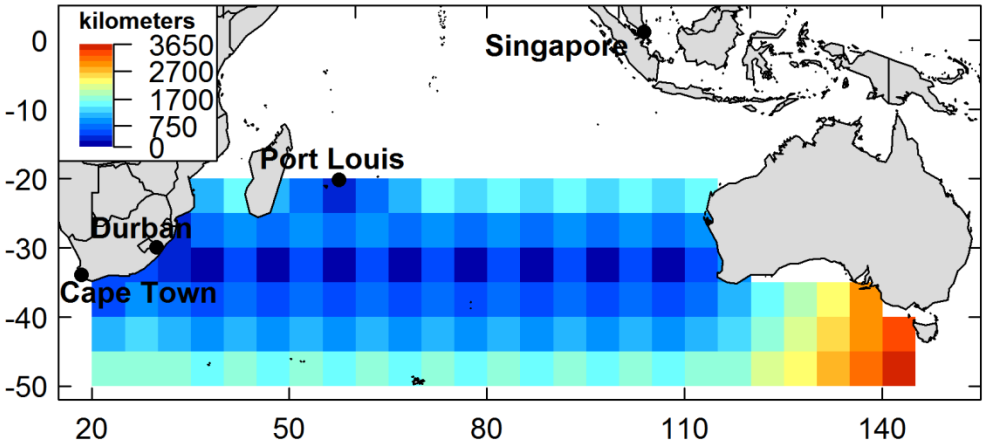

Figure 3.8 *The relative cost, approximated by the minimum distance from the nearest major port or approximated carrier vessel location, for Japanese and Taiwanese pelagic longline vessels. As we were unable to obtain data on the distribution of carrier vessels in time and space, carrier vessel locations were estimated from yearly maps from the Regional Observer Program (MRAG and CapFish, 2013, 2015, 2016) and assumed to remain static over time (see Appendix A.2 for details).*

3.4.3 Effort allocation strategy development and assessment

The strategy most related with observed effort in both fleets was the minimum variability strategy (No. 4, Table 3.4). The distribution of the mean modelled and observed effort was quite similar (Fig. 3.9 a - d). Furthermore, Pearson correlations between the mean modelled and observed effort for the Japanese fleet was 0.93 ($df = 115$, $p < 0.001$) and for the Taiwanese fleet it was 0.96 ($df = 77$, $p < 0.001$). Areas of high mean effort near Madagascar, south of Africa, and in the central eastern study area were identified for Japan, as well as areas off of east Africa and along the central study area for Taiwan.

Table 3.4 *Summary of AICs for linear models of effort allocation strategies and a random effect for cell (Equation 3.1) by pelagic longline fleet: Japan or Taiwan. "no." = reference number for a given strategy.*

fleet	no.	strategy	AIC	Δ AIC
Japan	1	balance of value and cost	15062.54	202.5
Japan	2	maximum value	15049.31	189.27
Japan	3	balance of value and variability	15027.71	167.67
Japan	4	minimum variability	14860.04	0
Taiwan	1	balance of value and cost	13272.65	539.55
Taiwan	2	maximum value	13277.13	544.03
Taiwan	3	balance of value and variability	13275.75	542.65
Taiwan	4	minimum variability	12733.1	0

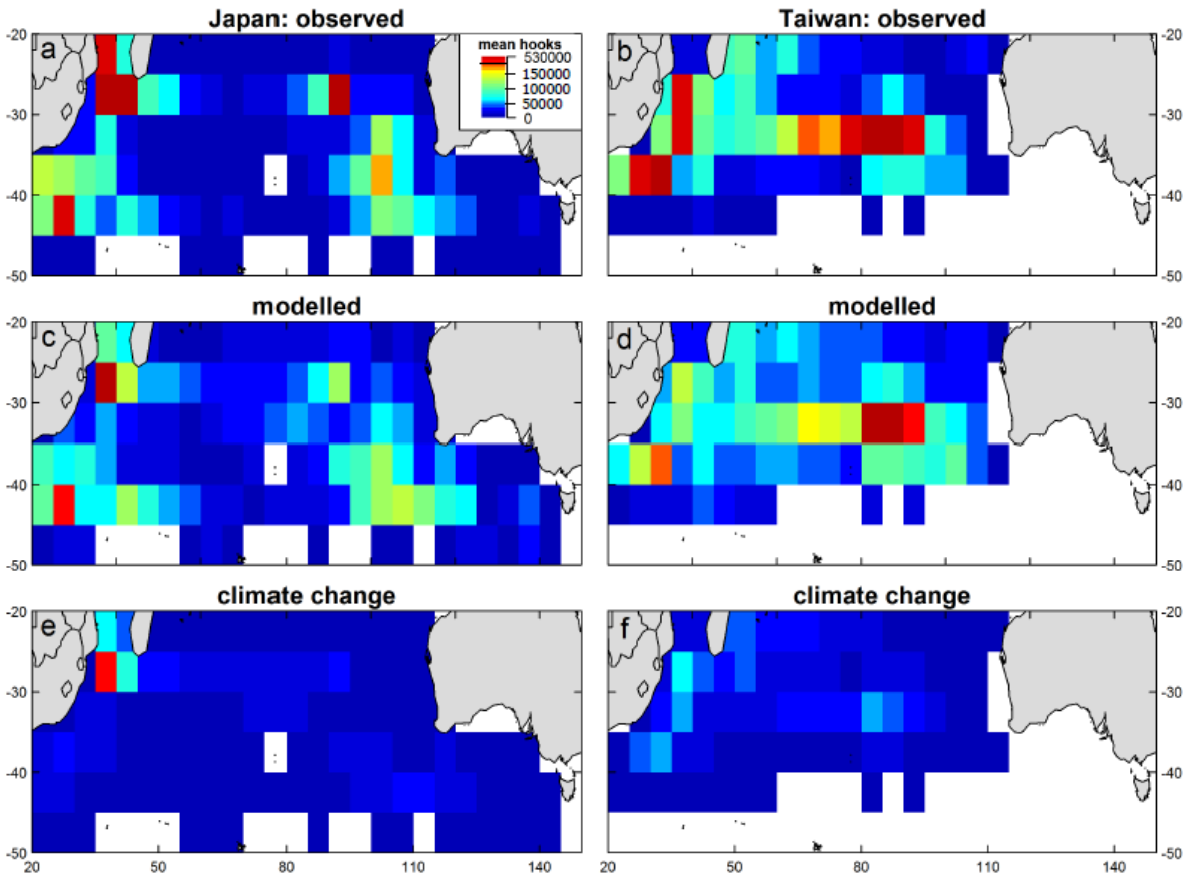

Figure 3.9 *Mean number of hooks (a, b) observed, (c, d) modelled, and (e, f) predicted with climate change for (a, c, e) Japanese and (b, d, f) Taiwanese pelagic longline fleets assuming a strategy targeting areas of 'minimum variability', as defined in Table 3.2. Dark blue indicates very low mean CPUE. Note broken scale indicated by the black line through the colorbar.*

Predictions under climate change indicate a strong decrease in the mean magnitude of effort across both fleets (Fig. 3.9e, f). Both fleets are predicted to remain in similar 'core' fishing areas, particularly in the western region, indicated by the observed data: south of Madagascar for Japan, off shore of eastern Africa for Taiwan. However, the cell located southwest of Madagascar, centered at ~ 42.5° E, 27.5° S, is predicted to become the strongest concentration of effort in this region across these fleets.

The mixed effects model for the minimum variability effort allocation strategy suggests very high variability in the effect of each cell, with the standard deviation being greater than the

variance for both fleets (Table 3.5). The intercept of these models indicates the minimum magnitude of effort a fleet will allocate to a cell, or the 'minimum threshold' for effort allocation. For the Japanese fleet, the threshold was much larger than that of the Taiwanese model. Species-specific strategy coefficients indicated that ALB and SBT were the primary and secondary targets of Japanese effort, respectively. This was followed by YFT and BET, which had a very small coefficient. For the Taiwanese fleet, BET was most heavily targeted, followed by SBT, then ALB, which had quite similar coefficients. Lastly, YFT had a very small coefficient. A small coefficient implies the associated tuna is a byproduct species for a given fleet in the study area.

Table 3.5 *Summary of effects from the mixed-effects model of the best effort allocation strategy for both Japanese and Taiwanese pelagic longline fleets: minimum variability. "cell id" indicates a unique identity for each cell, 'SD' = standard deviance. Coefficient values for the intercept and the effort allocation strategy value for each tuna species and the SE were converted by back-transforming the original model output, as the model assumes a lognormal distribution.*

	Effort (hooks)	
	Japan	Taiwan
Random effects		
Groups	variance (± SD)	
cell id	0.584 ± 0.764	0.259 ± 0.509
residual (error)	2.024 ± 1.423	1.840 ± 1.357
Fixed effects		
Variable	coefficient (± SE)	
intercept	2,212.924 ± 1.233	132.053 ± 1.469
ALB	14.832± 1.434	7.643 ± 1.748
SBT	4.545 ± 1.210	15.013 ± 1.166
YFT	1.747 ± 1.243	0.761 ± 1.562
BET	0.983 ± 1.311	78.870 ± 2.162

3.5 Discussion

Our approach to identifying effort allocation strategies of broad-scale multi-species fleets (Fig. 3.2) provides a novel tool and new insight into the potential impacts of climate change through an improved understanding of regional fleet behavior. Specifically, our effort allocation models identify a similar strategy of fishing in areas with predictable CPUEs, with a strong correlation between the predicted and observed values for each fleet. Yet these fleets differ in their relative targeting of each species as well as their minimum threshold for allocating effort (Table 3.5), resulting in distinct effort distributions. Our CPUE models predicted a decrease in the CPUE of three of the four tuna species with a mean decrease across species, and an increase in the uncertainty of all CPUEs. As we assumed fleets maintained the strategy which most accurately reproduced the historic distribution and magnitude of fishing effort; allocating effort to areas of low variability, increased variability in CPUEs resulted in less effort predicted to be allocated to each cell by both fleets (Table 3.4; Fig. 3.9e, f).

3.5.1 CPUE predictions given climate change

Although these new conditions likely do increase catch and decrease variability of some cells and periods, such as ALB in regions warming above 17 °C (Fig. 3.4a), the general trend is a decrease in the cross-species mean CPUE (Fig. 3.5). The decrease in ALB and SBT CPUE is due to the general increase in SST while decreased SSHa contributed to the reduced CPUEs of ALB, SBT, and YFT. High SSHa indicates stronger than average convergence (of eddies, gyres, or fronts), likely providing efficient foraging for mobile predators (Olson and Backus, 1985; Olson et al., 1994). The reduced SSHa projected with climate change suggests weaker convergence along these boundaries, resulting in more diffuse prey aggregations, decreasing foraging efficiency and growth in the long term. Countering this trend of smaller CPUEs, the

increase in BET CPUE is likely due to the relationship between SSTs in the mid-20s and moderately elevated CPUE (Fig 3g, h). This indicates a poleward shift in CPUE, in line with other studies on tuna distribution (Hobday, 2010) and catch potential (Cheung et al., 2010).

Given the broad distribution of these tuna species and our focus on the southern Indian Ocean, it is important to note the potential biases in these CPUE models. Three potential sources of bias are: i) imperfect data, ii) the spatial scale of the analysis, and iii) our modeling assumptions. Regarding the first issue, the possible misreporting of species-specific catch by the Japanese fleet could impact the modelled CPUE for tuna in this southern region (Polacheck and Davies, 2008). While this would have significant impacts on stock assessments, the number or weight of SBT potentially reported as YFT or BET would be relatively small compared to the total catches of YFT or BET (Polacheck and Davies, 2008). In restricting the spatial scale of our analysis to the southern Indian Ocean our study area does not include important tropical habitats, for BET and YFT in particular (Arrizabalaga et al., 2014). Not encompassing the range of environmental parameters creating core YFT habitat could explain why bathymetry, as opposed to SST, SSHa or Chl was selected as an important habitat parameter.

Regarding the spatial scale, much of the disagreement between the observed and modelled mean CPUE across species (Fig. 3.5a-d) relates to over-estimates of species-specific models in the cells along the edges of the observed catch for each species (Fig. A.1-A.4a-b). Specifically, for modelled Japanese CPUEs, higher than observed mean CPUE across species between 50-60° E correspond to cells outside of or near the edge of observed SBT, ALB and YFT catch (Fig. A.1-A.3), where one but not all of the focal species were observed caught. Over-estimated mean Taiwanese CPUE across species related to high modelled SBT CPUE in the northeast (Fig. A.2) and high modelled ALB, YFT and BET CPUE in the eastern edge of the

study area (Fig. A.1, A.3-A.4). On a broader scale, while excluding effort from the southern Atlantic and Pacific Oceans may eliminate important fleet information not captured by our model, including movement to and from the Atlantic through Cape Town (*David Japp, pers. comm.*), rising fuel costs have resulted in many vessels fishing in a single ocean (Hamilton et al., 2011).

Lastly, our modeling approach involves several important assumptions, directly impacting our results. One such assumption not discussed in the Methods section is that CPUE can be represented as a smooth surface. In creating each of the fishery parameters, we have made many assumptions, many of which are outlined in our methods. The GAM provides an optimal interpolation of the available data, balancing fit and smoothness in the spatial surface (Wood et al., 2006). At locations with few observations, the fitted surface may deviate from the observations as the estimation procedure balances the fit to surrounding areas with more data and the need for the statistical model to change in a smooth fashion in space. While this will produce increased deviations between observations and fitted values in these locations, the inaccuracy will be captured in the error around the spatial surface, and be reflected in any predictions made using the fitted model. Finally, our assumptions that species-specific CPUE habitat, targeting practices, and the identified effort allocation strategy would remain unchanged over time given climate change distinctly shape our predicted outcome and its interpretation. Despite these imperfections, these CPUE models enabled the development of fleet dynamics models that successfully reproduced the mean distribution and magnitude of fishing effort across the study region.

3.5.2 Species-specific value and costs estimate limitations

Our assumptions of a constant value for each species over time, as well as definition of cost, which does not change with time, and the immobility of carrier vessels are likely unrealistic. It would be preferred to develop a business model identifying key financial characteristics for each fleet, incorporating detailed information on fleet composition, maintenance and bait costs, the fuels used, freezer capacity, and the dynamics of carrier vessels. However, these approximations were sufficiently informative to explore the association with fishing effort and the impact of climate change given these assumptions. The four effort allocation strategies we explored were by no means comprehensive but representative of broad concepts in the distribution of limited resources based on the fishery parameters we have developed. We did not incorporate known challenges for these fleets, including a lack of young crew members and difficult acquiring a bank loan to construct replacement vessels for the Japanese fleet (Hamilton et al., 2011) and an overall reduction in the number of registered vessels as part of an effort to reduce tuna-fishing overcapacity (Hamilton et al., 2011; Moreno and Herrera, 2013). Although the absence of this information limits the inference available through our analysis, our approximations of the relative costs and value of different areas enabled this first attempt to identify the factors influencing the dynamics of these major pelagic longlines.

3.5.3 Shared and fleet-specific behavior

The importance of minimizing variability for both fleets suggested by the selected effort allocation strategy is not surprising, as the dynamics of other longline fleets are impacted by risk (Dowling et al., 2013; Dowling et al., 2012). In describing variability as the SE from each species-specific GAM, this value encompasses both process variability and observation error.

This makes it difficult to attribute SE to a single variable or interaction between variables. Consider the high uncertainty of SSHa ~0.4 for YFT CPUE as opposed to SSHa ~1.0 for the same species (Fig. 3.4f). The relatively high uncertainty around SSHa 0.4 appears to few data within the observed fished area (Fig. 3.3d, Fig. 3.5a, b) but could also indicate an inconsistent relationship between observed CPUE and SSHA~ 0.4, . Regardless of exact source of CPUE prediction uncertainty, the impact of environmental variation on tuna CPUE is well known in the tropics (Corbineau et al., 2008; Corbineau et al., 2010; Lan et al., 2013). It is also reasonable that the change in environmental conditions projected with climate change (Fig. 3.3) would produce both greater standard errors in our models and increase the variability in our CPUE predictions with climate change (Fig. 3.6, A.5-A.8). Other studies have demonstrated a strong preference of fishers to fish in known areas or a resistance to fish new areas has been observed previously (Davies et al., 2014), even in the face of shifting species distributions (Pinsky and Fogarty, 2012). We did not explicitly evaluate the preference of fishers to return to a particular cell nor did we model areas with no previously observed effort. As seasonal oscillations in the broad-scale distribution and magnitude of effort by these fleets has been observed (Michael et al., 2015), it is possible that some degree of spatial fidelity is shown by these fleets, albeit outside of the scope of the current study.

Fleet-specific tuna targeting and minimum thresholds for allocating effort produce the unique distributions of these two fleets. The impact of these targeting and threshold differences is seen by comparing the differences between the mean inverse standard error and mean effort plots (Fig. 3.6, Fig. 3.9) and the intercept and coefficients for the fitted model (Table 3.5). The Japanese fleet has a high minimum threshold (linear model intercept; Table 3.5) for effort and distributes effort in two distinct east-west patches (Fig. 3.1, 3.9). This is in direct contrast with

Taiwan, with a lower threshold (Table 3.5) and relatively uniform, more diffuse distribution of effort, in magnitude and across longitudes (Fig. 3.1). This indicates that Japanese targeting practices are focused on fishing in particular regions 'worthy' of allocating a very large minimum threshold of effort while Taiwanese effort is more diffusely distributed. Indeed, Taiwanese vessels are known to adjust their behavior, including changing target species, altering vessel freezing temperatures, and retaining non-target species to maximize the value of their catch (Hamilton et al., 2011).

The strength of species-specific effort allocation strategy coefficients likely reflects the co-occurrence of common and rare target species. For the Japanese fleet, the ranking of ALB as the primary and SBT as the secondary target species likely reflects the greater abundance of ALB than SBT as well as their overlap in the study area (Fig. 3.5). As 30% of the global Japanese fleet has participated in the SBT fishery since 1983, at least through 2006 (Polacheck and Davies, 2008), it is reasonable to assume that the majority of Japanese vessels in our focal region frequently target SBT, with ALB as a byproduct species. This is in agreement with other research (Moreno and Herrera, 2013; Tuck et al., 2003). YFT and BET are likely to be byproduct species or seasonally targeted when ALB and SBT are less common or spawning (Michael et al., 2015). Very low variability predicted with climate change for both ALB and BET in the same cells likely resulted in the large amount of effort predicted to occur south and west of Madagascar (~42.5° E, 27.5° S).

In the Taiwanese fleet, heavy targeting of lucrative BET may reflect a shift in Taiwanese effort from the Atlantic, when BET quota in this region was reduced in 2006 (Chen, 2012) or targeting of a species with the lowest maximum (and mean; not shown) variability (Fig. 3.6, Fig. A.8). Given the seasonal migrations of the second and third target species, SBT and ALB,

respectively, BET may offer a relatively stable target. Lastly, YFT appear to be relatively weakly targeted by the Taiwanese fleet. Additionally, the relative value of each species: SBT > BET > YFT > ALB (Fig. A.9) as well as fleet specific market connections likely interact to influence targeting by both fleets. Lastly, it is important to note that by using a model fitted with historical data, this approach assumes that these fleets will not change their targeting practices from the time period that we have studied and used to make our predictions.

3.5.4 Opportunities and applications

The work here and our approach in general can be further developed by incorporating different aspects of fisher behavior and socio-economic aspects of the fishery (Pascoe et al., 2013; Van Putten et al., 2012). Accounting for opportunity costs (Dowling et al., 2012) and the interactions between fishers (Maury and Gascuel, 2001) could more accurately depict fisher behavior. While the cost-earnings of smaller longline fleets have been described (Hamilton et al., 1996), information to this level of detail is not currently available, to our knowledge, for either of the fleets modelled in this paper. As broad-scale effort in these fleets has a clear seasonal cycle (Michael et al., 2015), incorporating seasonality into the currently annual model could capture important intra-annual variation. An increasing understanding of fisher spatial behavior (Davies et al., 2014; Pinsky and Fogarty, 2012), may also increase the accuracy of these models. Regarding tuna distributions, greater detail on the spatial ecology of tunas (Dueri et al., 2014; Lehodey et al., 2015), or integrating stock-assessment models could create more realistic CPUE predictions. Given the necessity of multi-disciplinary broad-scale collaborations to promote tuna harvest at sustainable levels (Hobday et al., 2015a; Salinger et al., 2013), tools such as this are needed to facilitate interaction and communication between stakeholders. Projections from models such as these are also useful for exploring potential future interactions with other

fisheries or sensitive bycatch species. Forecasting tools in fisheries are already in use (Hobday et al., 2011; Howell et al., 2008), and these can be extended in the future with the development of fleet dynamics models that account for changing fisher behavior.

3.6 Acknowledgements

We are grateful for the comments and suggestions of Miguel Herrera and Gerard Domingue (IOTC), other IOTC staff, and David Japp (CapMarine) regarding these fishing fleets. Mike Sumner (Australian Antarctic Division) greatly assisted in the aggregation of environmental data and development of the figures.

Appendix A Additional information on data used in fleet dynamics models

A.1 Fisheries data standardization

As the annual sums of Taiwanese monthly logbook catch data were generally less than the yearly catch data, the fishing effort was raised by the ratio of reported yearly catch to the annual sum of monthly logbook catch (Campbell, 2003; Tuck, 2004). We also adjusted the tuna catch weights in the logbook data to match those of the yearly data in the same way. As Japanese data are believed to be comprehensive, the data were not adjusted (Campbell, 2003; Tuck et al., 2015). Although possible inaccurate reporting of SBT catch by the Japanese fleet may have led to some misreported catches of tuna species and/or fishing effort location (Polacheck, 2012), it was beyond the scope of this study to account for this issue. To our knowledge, data to perform this correction do not exist. We restricted our analysis to the period 1998 through 2011.

As only the number of fish caught in each 5°×5° cell by month was available for the Japanese fleet, we estimated the mean weight of each species in space and time using the corresponding Taiwanese data. We used a Generalized Additive Model (GAM) to describe the relationship between the mean weight of each species by the outer (tensor) product of latitude and longitude by year as a factor:

$$weight / number = s(longitude * latitude, by = year) \quad (1)$$

where 's' specifies a product spatial smooth. This created a unique spatial surface for each year, allowing changes in the mean size of individual fish of each species captured at a given location to vary over years (Maury et al., 2001). A Gamma distribution using a log link function produced relatively normally distributed residuals for all species. The fitted GAM was then

applied to the Japanese data. Given difficulties predicting weights in regions with little / no overlap in species-specific catch due to differences in the distribution and targeting of Japanese and Taiwanese effort (Michael et al., 2015; Tuck et al., 2003), we limited the modelled mean weights to $^1/_3$ of the maximum observed weight of an individual for each species as reported in FishBase (Froese and Pauly, 2015): ALB 60kg, SBT 260kg, BET 210kg, YFT 200kg. These values are equal to (ALB), or slightly above (SBT, YFT, BET) observed Taiwanese CPUEs. This reduction agrees with the observed maximum mean weight of albacore caught by the Taiwanese fleet in this region. Throughout the manuscript, references to 'observed Japanese CPUE data' include the weights estimated using the above methods.

A.2 Defining costs: carrier vessel location

In the six years of currently viewable carrier vessel location data (2010-2015), there was a constant band of vessels around 12° S and 34° S, outside of EEZs. While the reason for these bands is unclear, their reliable location lead us to assume that the band within the study area (34° S) was occupied consistently and that carrier vessels are not randomly distributed. While transhipment locations indicate a relatively solid distribution of transhipments occurring across this band, we chose to place vessels every 10 degrees (every-other cell) as a conservative estimate for the number of vessels actively transferring at a given time. As we have no information on the movement of carrier vessels, we assumed transfer locations were static. The placement of vessels along this line had relatively little impact on the cost-surface, as the low cost of this latitude remained constant. Our definition of costs involves broad but practical assumptions given the current lack of information on fleet composition (e.g. types of fuel and bait used), the movement of individual vessels, and our unsuccessful attempts to obtain carrier vessel data.

Given the large size of these vessels and the long periods spent in a relatively homogenous (ice-free, open water) environment (Hamilton et al., 2011), we assume that other operational costs are roughly constant with respect to location and did not explore the possibility of a change in carrier vessel location, port, or a non-linear relationship between distance and cost. We assumed that any change in transport cost would be linearly related to distance.

A.3 Species-specific CPUE and inverse SE plots

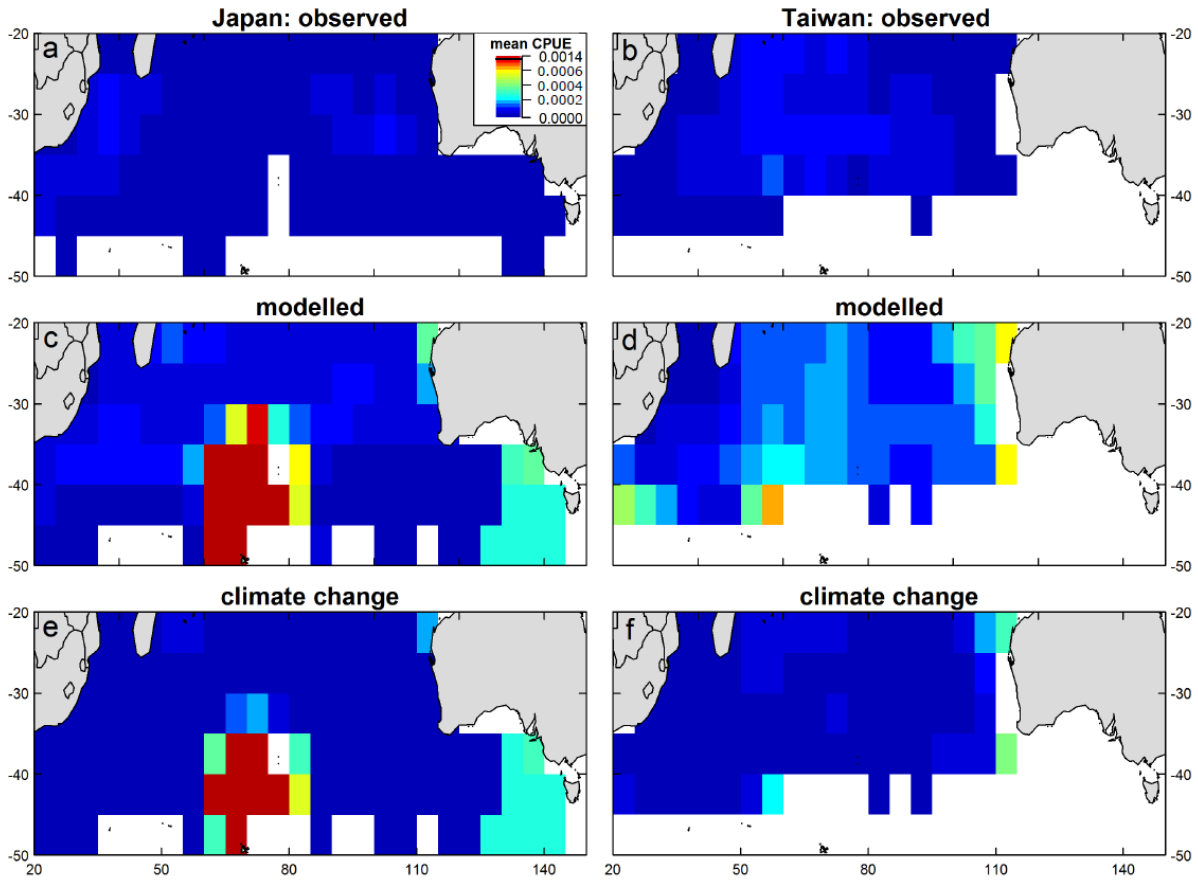

Figure A.1 *Arithmetic mean CPUE of ALB (a, b) observed data, (c, d) modelled, and (e, f) predicted with climate change CPUE models for (a, c, e) Japanese and (b, d, f) Taiwanese pelagic longline fleets. Dark blue indicates very low mean CPUE. Note broken scale indicated by the black line through the colorbar.*

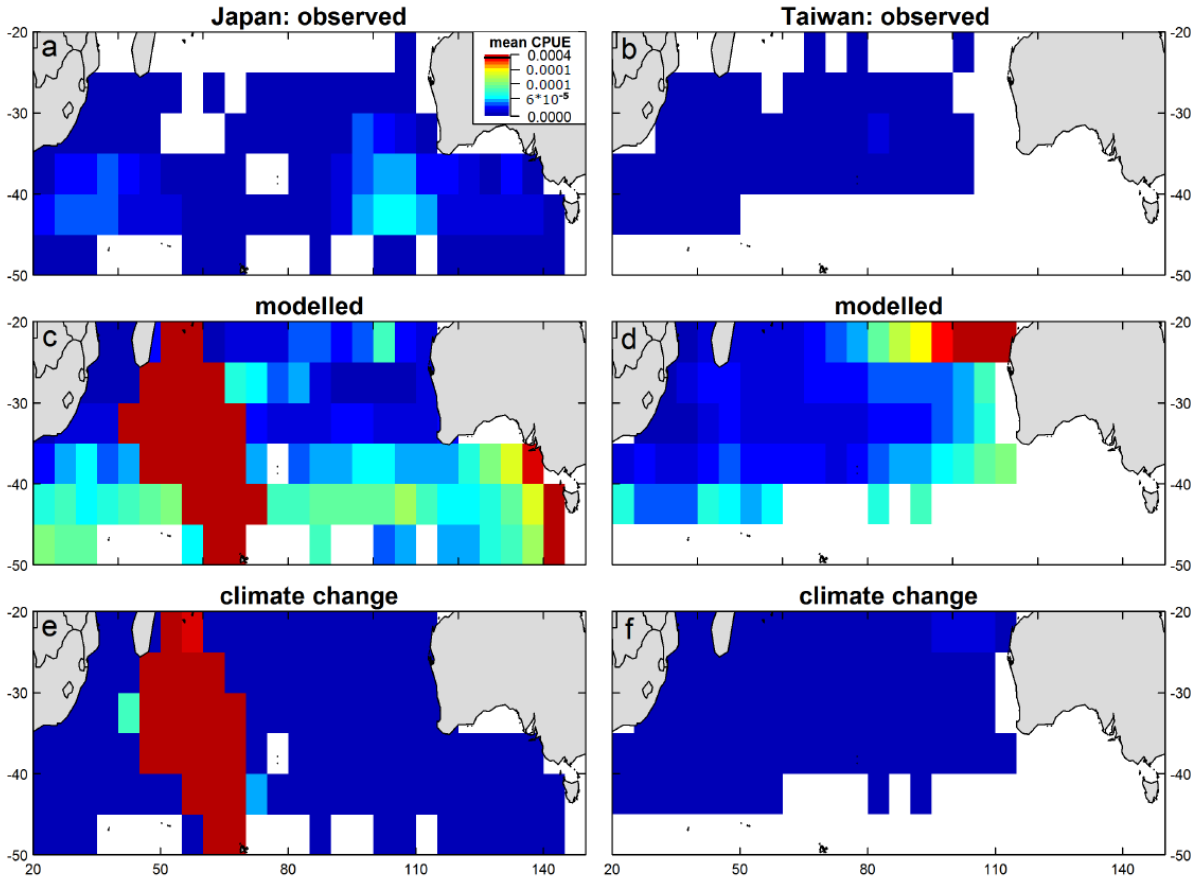

Figure A.2 *Arithmetic mean CPUE of SBT from (a, b) observed data, (c, d) modelled, and (e, f) predicted with climate change CPUE models for (a, c, e) Japanese and (b, d, f) Taiwanese pelagic longline fleets. Dark blue indicates very low mean CPUE. Note broken scale indicated by the black line through the colorbar.*

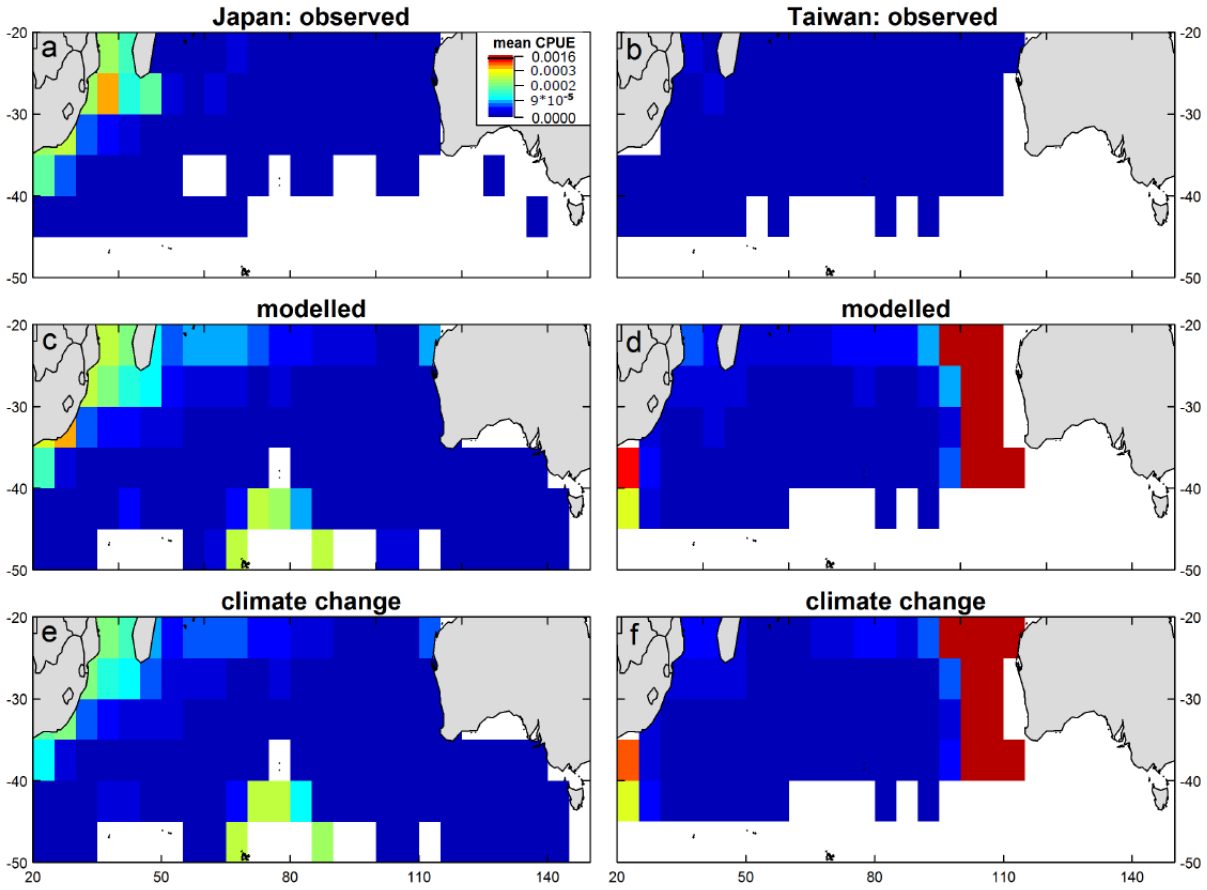

Figure A.3 *Arithmetic mean CPUE of YFT (a, b) observed data, (c, d) modelled, and (e, f) predicted with climate change CPUE models for (a, c, e) Japanese and (b, d, f) Taiwanese pelagic longline fleets. Dark blue indicates very low mean CPUE. Note broken scale indicated by the black line through the colorbar.*

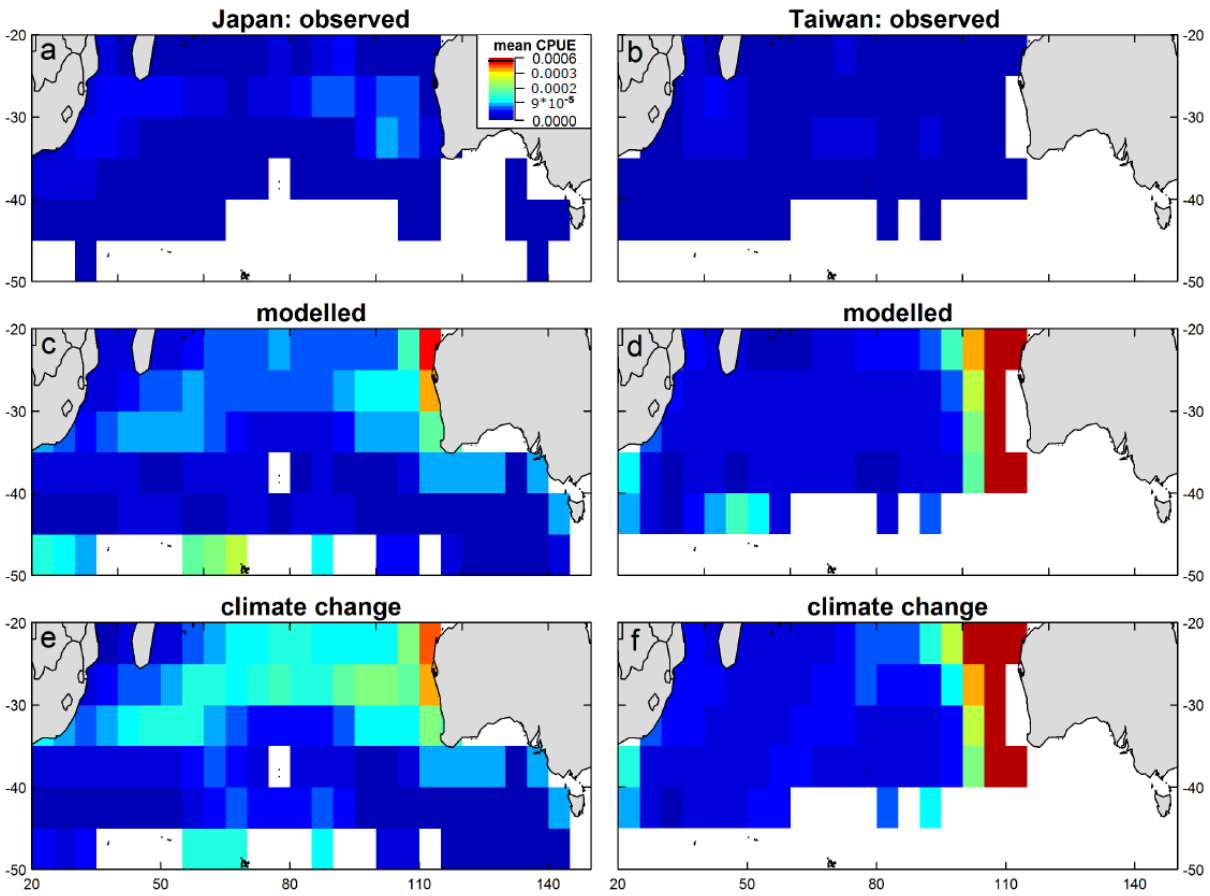

Figure A.4 *Arithmetic mean CPUE of BET (a, b) observed data, (c, d) modelled, and (e, f) predicted with climate change for (a, c, e) Japanese and (b, d, f) Taiwanese pelagic longline fleets. Dark blue indicates very low mean CPUE. Note broken scale indicated by the black line through the colorbar.*

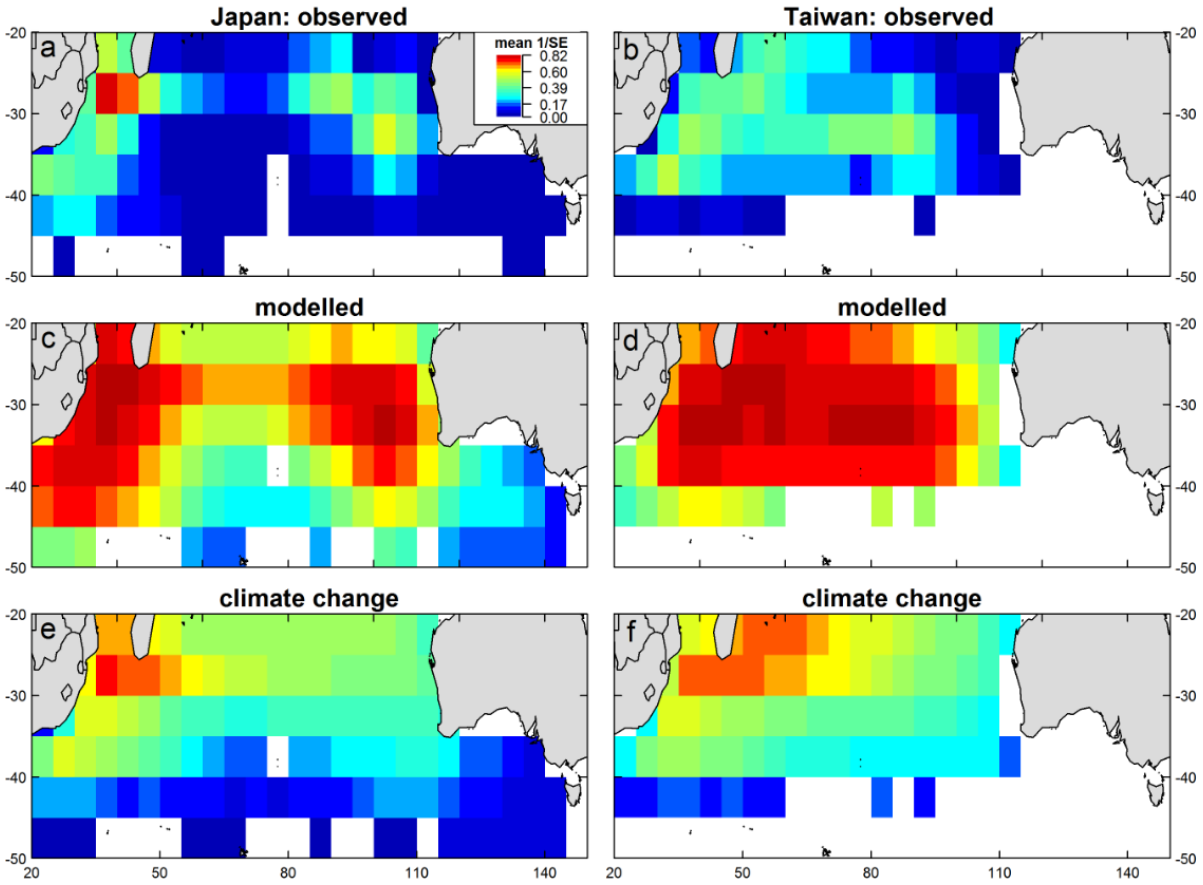

Figure A.5 *Arithmetic mean of the inverse SE of CPUE for BET from (a, b) observed data, (c, d) modelled, and (e, f) predicted with climate change for (a, c, e) Japanese and (b, d, f) Taiwanese pelagic longline fleets. Dark blue indicates very low mean CPUE.*

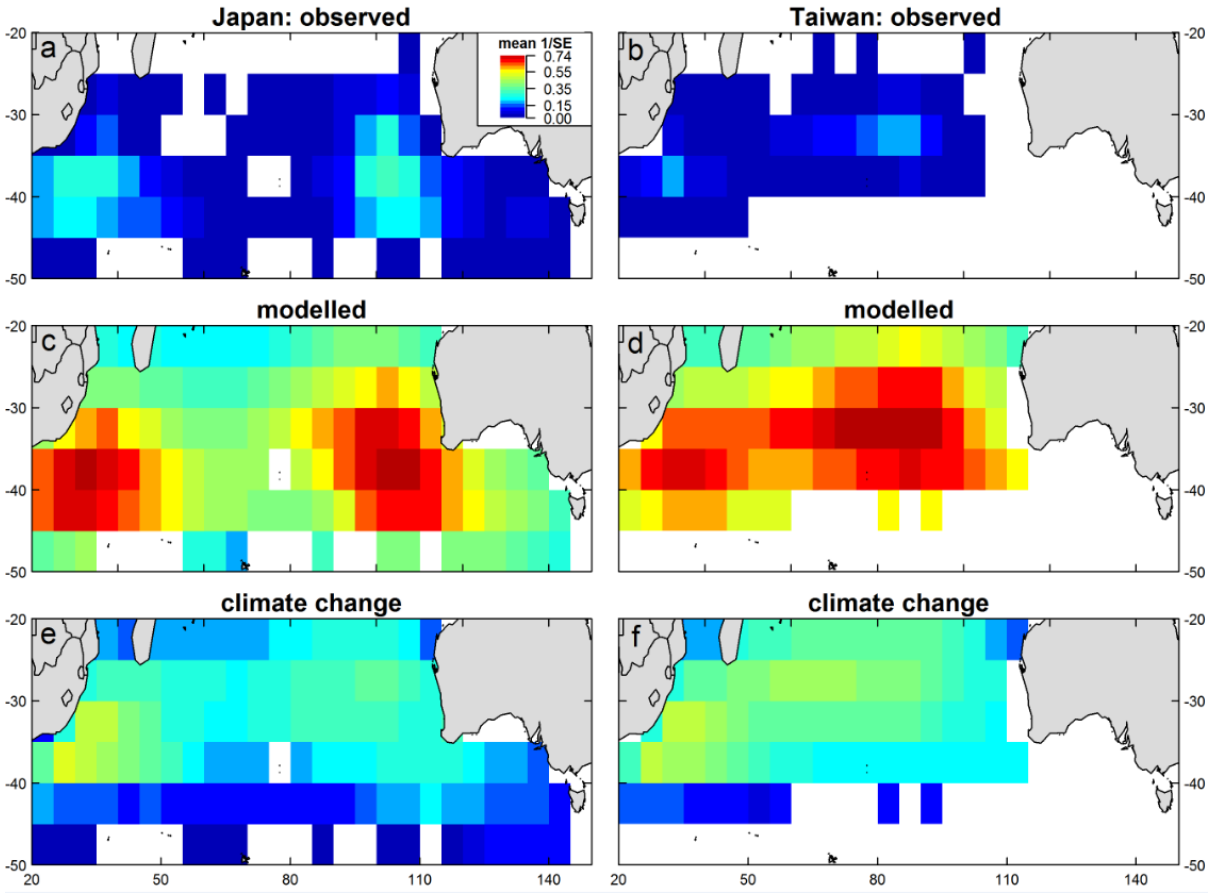

Figure A.6 *Arithmetic mean of the inverse SE of CPUE for SBT from (a, b) observed data, (c, d) modelled, and (e, f) predicted with climate change for (a, c, e) Japanese and (b, d, f) Taiwanese pelagic longline fleets. Dark blue indicates very low mean CPUE.*

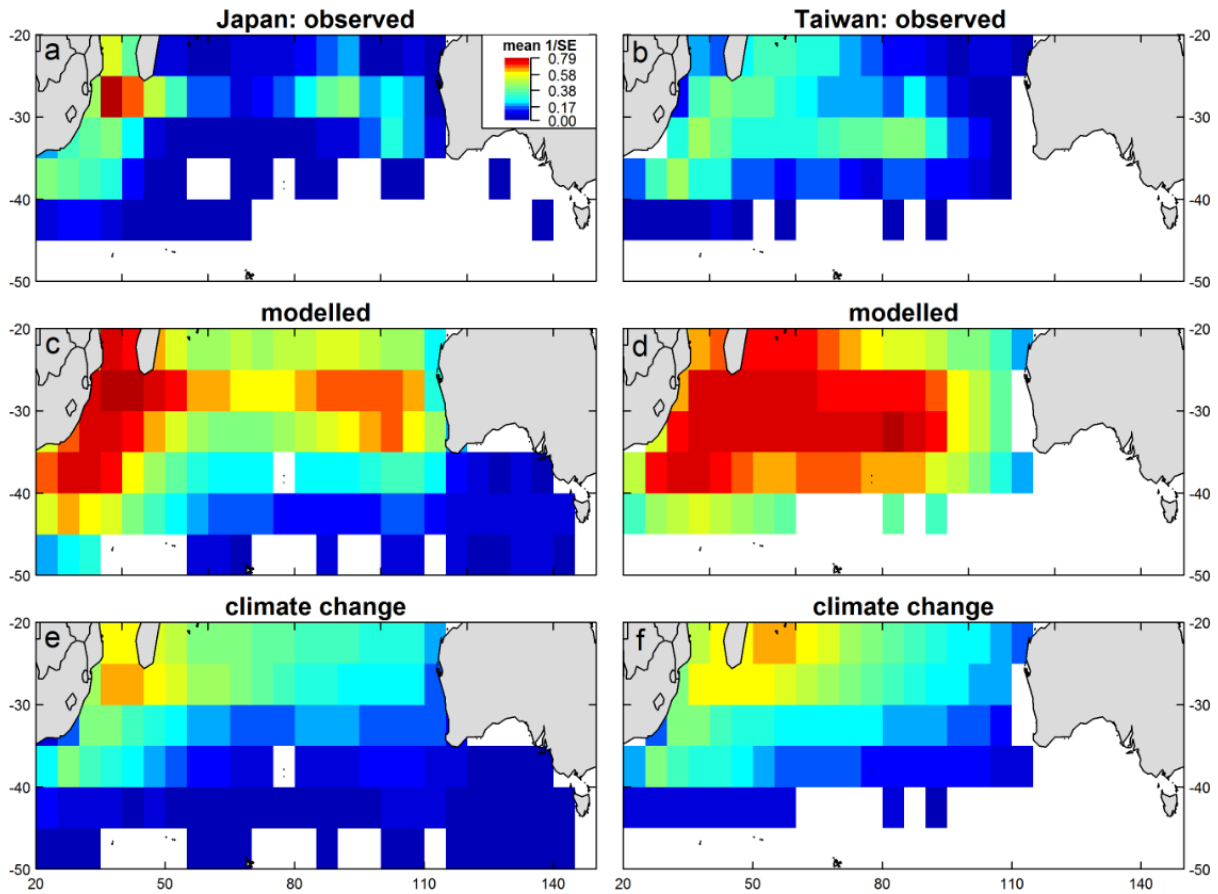

Figure A.7 *Arithmetic mean of the inverse SE of CPUE for YFT from (a, b) observed data, (c, d) modelled, and (e, f) predicted with climate change for (a, c, e) Japanese and (b, d, f) Taiwanese pelagic longline fleets. Dark blue indicates very low mean CPUE.*

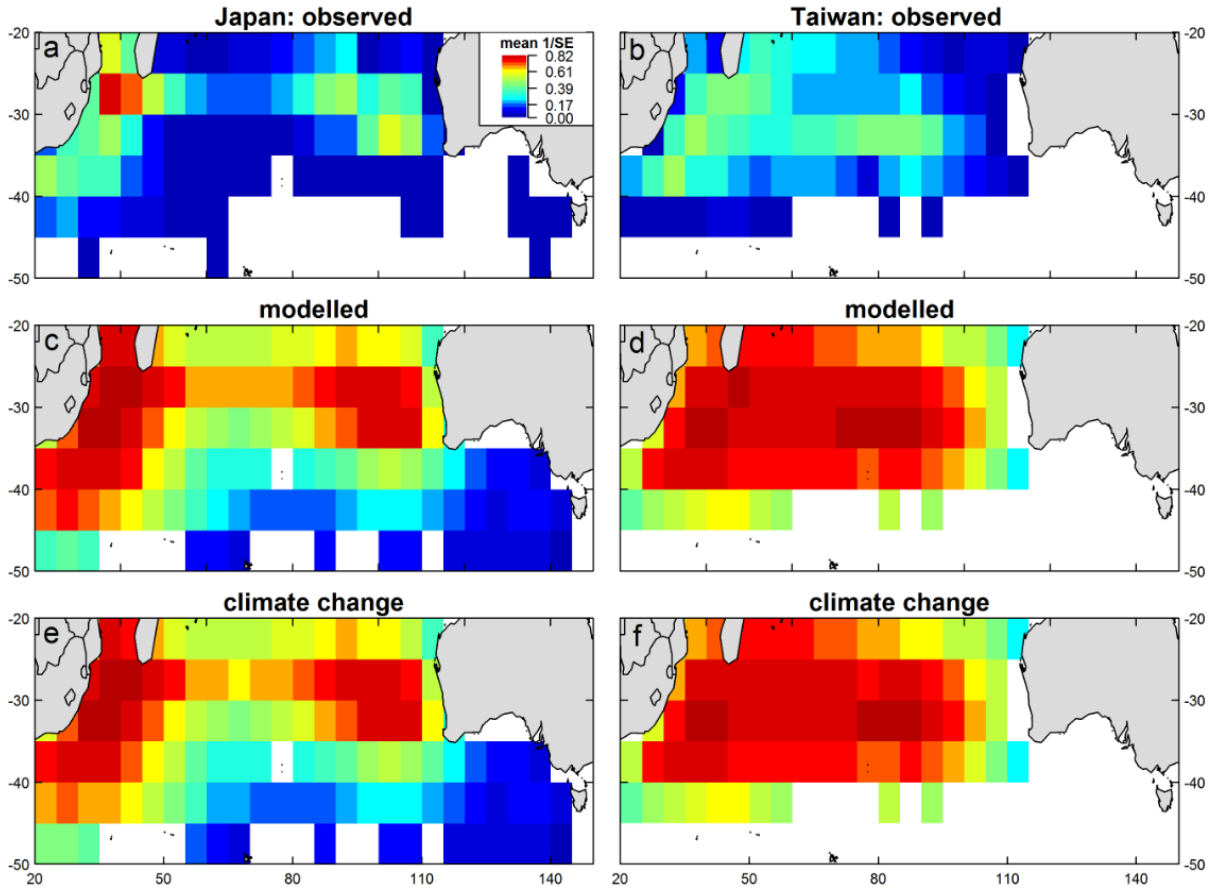

Figure A.8 *Arithmetic mean of the inverse SE of CPUE for BET from (a, b) observed data, (c, d) modelled, and (e, f) predicted with climate change for (a, c, e) Japanese and (b, d, f) Taiwanese pelagic longline fleets. Dark blue indicates very low mean CPUE.*

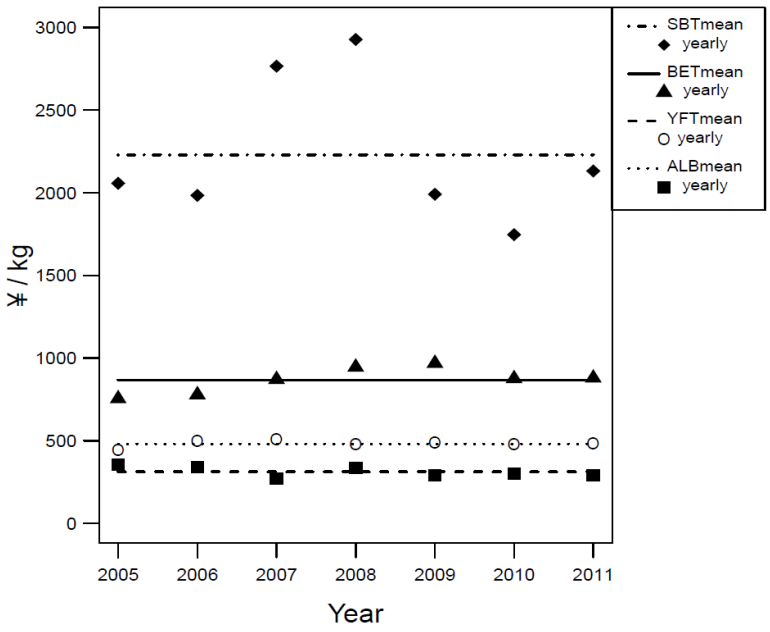

Figure A.9 *Annual (symbols) and annual average value (yen per kilogram; lines and dashes) of the four focal tuna species, from 2005 through 2011. Data were obtained from three statistical yearbooks, retrieved from the Japanese Ministry of Agriculture, Forestry and Fisheries (http://www.maff.go.jp/e/index.html).*

4 Relative impacts of the environment and fisheries bycatch on an albatross population

4.1 Abstract

Albatross populations are impacted by multiple factors, including environmental variation and fisheries bycatch. For the effective management of albatross populations, it is necessary to understand the relative impact of each of these factors. Recent studies have identified that fisheries, environmental correlates, and density-dependence can shape the viability of populations. An integrated modeling approach, incorporating multiple data sources, can further the understanding of albatross demographics by simultaneously incorporating error from all components of modelling and distinguishing between variability related to one factor (e.g. the environment) from that of another factor (e.g. density-dependence). We apply an integrated population model quantifying the impact of environmental conditions, fisheries, and density-dependence on young albatross for a black-browed albatross colony breeding on Kerguelen Island, southern Indian Ocean. The model is structured by sex, age-class, breeding stage, and reproductive history of individual albatross, with a 5˚ × 5˚ spatial scale and monthly temporal scale. It also estimates the bycatch of each of five super-fleets (fleets grouped by gear-type and reported bycatch rates): (i) Japanese mitigated pelagic longline south of 30° S, (ii) other pelagic longline, (iii) demersal longline, (iv) trawl, and (iv) illegal, unreported and unregulated (IUU) demersal longline. Analyses indicate that high bycatch in the mid-1990s to early 2000s relates to strong population decline, with the majority of bycatch attributed to IUU demersal longline effort, although the modelled IUU bycatch rate differs from the observed. In line with other studies on this population, we find that warmer ocean temperatures during the incubation period

favors higher breeding success, improving estimated demographic rates for early life stages. The relative impact of the environment appears to be weaker than that of bycatch for the period and population evaluated. The ability to differentiate bycatch by super-fleet and the relative impacts of environmental conditions during different periods of population dynamics provides novel insight into the factors currently influencing this population. Results from this model can be used to identify factors impacting historic population trends and enhance the ability to manage vulnerable populations impacted by multiple factors.

4.2 Introduction

The trajectory of albatross abundance is the result of multiple factors, including historical harvesting, ongoing environmental variation (Chambers et al., 2011; Inchausti et al., 2003; Pinaud and Weimerskirch, 2002), interactions with fisheries (Robertson et al., 2014; Tuck et al., 2001), and demographic feedbacks (Fay et al., 2015). As long-lived, delayed maturity and slow-reproducing species, slight changes in adult mortality can have a strong impact on the population growth rate. Thus, factors impacting adult mortality often drive population trends. Managing albatross populations, many of which are endangered or threatened (Croxall et al., 2012), requires an understanding of the factors and their directional impact on population growth. However, identifying such factors often requires detailed demographic data. Due to difficulties in regularly accessing albatross colonies, which are often in remote and rugged locations, such data are not always available.

Fortunately, detailed demographic data on a black-browed albatross (BBA) colony on Island of Kerguelen, in the Southern Indian Ocean have been collected since 1979. The summer / breeding season diet of Kerguelen BBA includes fish and squids, and their foraging distribution

is restricted to the eastern Kerguelen shelf (Cherel et al., 2000; Cherel et al., 2002; Delord et al., 2013; Pinaud and Weimerskirch, 2002; Fig. 4.1a). During winter and non-breeding periods, most birds occur off southern Australia, while a few travel to western New Zealand or southwest of South Africa (Delord et al., 2013; Fig 1b). Globally, BBA have a circumpolar distribution in the Southern Ocean, breed on many sub-Antarctic islands during the austral summer (ACAP, 2012) and are listed as near-threated according to IUCN criteria (Birdlife International, 2014).

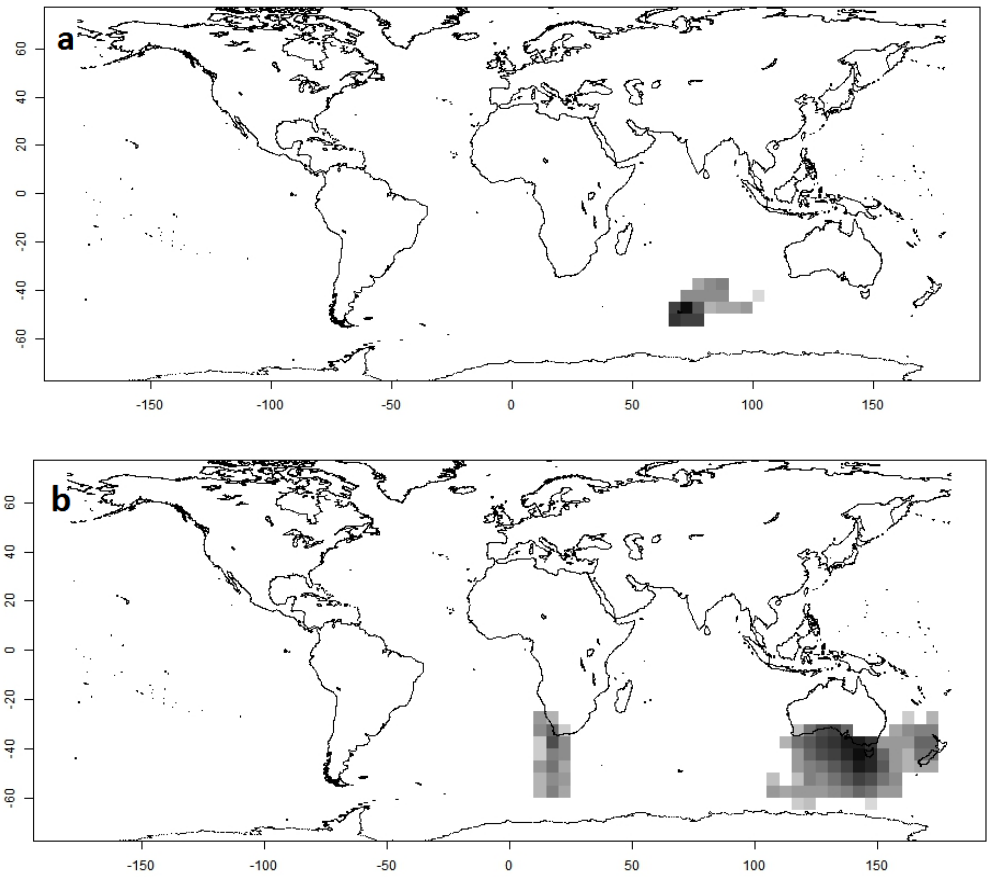

Figure 4.1. *Relative at-sea distribution of breeding black-browed albatross during the (a) rearing and (b) winter or post-breeding periods.*

Recent studies of this population have identified relationships between environmental factors and fishing effort. Regarding environmental associations, warm sea-surface temperature

(SST) around Kerguelen during the breeding period relates to increased breeding success and adult survival (Rolland et al., 2008; Rolland et al., 2010) and population growth rate (Rolland et al., 2009b). This contrasts with relationships in the wintering grounds, where productivity (positive SOI) or warm SST in the winter preceding breeding relates to reduced breeding success (Rolland et al., 2008; Rolland et al., 2010), population growth rate (Rolland et al., 2009b), and survival of inexperienced adults (Nevoux et al., 2007). When compared to BBA breeding on South Georgia (southern Atlantic Ocean) where the regional environmental variability is greater than around Kerguelen, the Kerguelen population has relatively higher breeding success but lower survival (Nevoux et al., 2010a).

In the Kerguelen Island BBA colony, a negative relationship of adult survival with longline effort (implicating bycatch) in the wintering grounds has been identified (Rolland et al., 2010). However, this impact was essentially equal to a positive relationship of warm SST during the early breeding season, resulting in no net change in adult survivorship. While the same study identified a strong, positive impact of trawl effort near the breeding grounds on breeding success (implicating enhanced foraging opportunities on offal), this fishery is no longer active. Compared to other albatross breeding in the Indian Ocean, this colony is unique in the observed association of breeding success and adult survival with fisheries and environmental covariates (Rolland et al., 2010). These complicated relationships make it difficult to attribute an observed change in the population to either or all covariates, particularly when the response could be nonlinear (Barbraud et al., 2011). Additionally, the impact of a given factor on demographics can be masked or amplified by other factors, such as density-dependence (Fay et al., 2015; Maunder, 2004).

Of the studies assessing environmental and / or fisheries impacts on albatross populations, most have quantified these relationships outside of the demographic model framework, then incorporated the resulting parameter into the demographic model (e.g. Barbraud et al., 2011; Nevoux et al., 2007; Rolland et al., 2009b; Rolland et al., 2010). Here, we apply an integrated analysis framework; incorporating all environmental, demographic, and fisheries data into the estimation framework, allowing the ability to distinguish between and quantify the relative contribution of multiple covariates on population. This approach is used in fisheries stock assessments (Maunder and Punt, 2013; Methot Jr and Wetzel, 2013) and in studies on albatross populations (Francis and Sagar, 2012; Thomson et al., 2015; Tuck et al., 2015). This approach has provided important insights into the factors driving historic demographic patterns and, in the case of Thomson et al. (2015), enables foresight into the future population trajectory.

In this study we apply an integrated population model (Thomson et al., 2015; Tuck et al., 2015) to Kerguelen BBA to assess the individual and cumulative impacts of the environmental variation and fisheries bycatch on population dynamics. This model incorporates environmental impacts on breeding success, the spatial overlap, and probability of bycatch in multiple fishing fleets as well as density-dependence on demographic rates. The relative impact and level of bycatch by fleet is assessed and the level of confidence in these estimates is also evaluated. This integrated approach can provide valuable insights into the relative impact of the environment and fisheries on a near-threatened albatross population, and will provide information to assess and manage this population.

4.3 Methods

4.3.1 Data sources

4.3.1.1 Demographic data and parameter estimation

Demographic data have been collected from 200 annually monitored nests at the approximately 1,000 breeding pair colony at Cañon des Sourcils Noirs, Kerguelen Island (48.24° S, 68.218° E, Fig. 4.2; Barbraud et al., 2011; Rolland et al., 2008). From 1967, adults and chicks were ringed with stainless still rings and since 1979 a capture-mark-recapture program has been undertaken annually between October and March. Most rings of breeding birds were checked in October just after laying. Two additional visits to monitored nests in late December and late March allowed determining the breeding success of each pair. Each year, all unringed breeding individuals found in the study area and all chicks were ringed just before fledging with a stainless steel band.

Using these data, multi-event capture-mark-recapture models were used to calculate demographic parameters (survival probability, breeding probability, success probability) for the period 1979-2013 (Pradel, 2005)[1]. These models incorporate uncertainty in the state (e.g. successful or failed breeder) of an individual at a given time. As the relationship between states and events is probabilistic, these models are within the Hidden Markov model family (Pradel, 2005). The model structure of the multi-event capture-mark-recapture model was similar to Barbraud et al. (2013) for wandering albatrosses. Juvenile survival until age 5 was estimated using a multistate capture-mark-recapture model following Lebreton & Pradel (2002) and

[1] Estimation of demographic parameters using multi-event capture mark recapture models was performed by Christophe Barbraud; Centre d'Etudes Biologiques de Chizé - Centre national de la recherche scientifique / Universite La Rochelle, France

Nevoux et al. (2010b) for the period 1967-2002. Juvenile demographic data for the years 2003-2013 were excluded since recruitment of individuals from these cohorts was not terminated (Nevoux et al., 2010). Our initial model for adults was a model were survival, breeding probability, success probability, capture probability and state assignment probability were state and time dependent. From this model, we first tested for temporal trends in detection probability and state assignment probability by fitting models where these probabilities varied according to a quadratic (or linear) trend on a logit scale as follows:

$$log\left(\frac{\theta}{1-\theta_t}\right) = \ logit(\theta_t) = a + b * T_t + c * \ T_t^2$$

where θ is the parameter of interest, a is the intercept, b and c are the slopes of the linear and quadratic terms, respectively, on the logit scale. We then tested for state dependence on the demographic parameters. Model selection was performed using the AIC and maximum likelihood estimates for demographic parameters were obtained from the program E-SURGE 1.8.4 (Choquet et al., 2009). These demographic estimates are used by the population model (below) to estimate the virgin (not impacted by fisheries) population demographic parameters.

4.3.1.2 Distribution at-sea data

Distribution at-sea was modelled as the utility distribution (e.g. Weimerskirch et al., 2015) for 13 different categories of sex, time of year, breeding status, and age (Appendix B.1, Table B.1). Breeding periods are based on those reported in Delord et al. (2013).

4.3.1.3 Fishing effort data

Given their relatively broad distribution, Kerguelen BBA are likely to interact with a broad range of fishing fleets. Albatross foraging around longline or trawl fishing activities can become hooked or entangled in fishing gear resulting in bycatch (Brothers, 1991; Croxall, 2008;

Sullivan et al., 2006). Monthly reported effort data in 5° x 5° spatial cells were acquired from the Indian Ocean Tuna Commission (IOTC), the Secretariat of the Pacific Community (SPC), the International Commission for the Conservation of Atlantic Tunas (ICCAT), Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), the French Museum of Natural History (French and Ukrainian trawl fleets within the Kerguelen French Exclusive Economic Zone), and the national fishing agencies of South Africa, New Zealand and Australia. As data within the Kerguelen French Exclusive Economic Zone did not include spatial coordinates, the location of effort relative to 5° x 5° spatial cells was estimated based on Weimerskirch et al. (2000). Data from Namibia and South American countries were obtained from Tuck et al. (2015). Further refinements to the effort data used in Tuck et al. (2015) are detailed therein and available at: DRYAD entry: doi: 10.5061/dryad.7f63m. These refinements were based upon updated publicly available effort data from the respective Regional Fisheries Management Organization. See Appendix B.2 for details on effort refinements regarding southern Indian Ocean fleets and Table B.2 for all fleets included in the model.

Effort was grouped into five 'super-fleets', composed of fleets from multiple nations based off gear type and reported bycatch rates as follows: (i) Japanese mitigated pelagic longline south of 30˚ S, (ii) other pelagic longline, (iii) trawl, (iv) demersal longline, and (iv) illegal, unreported and unregulated demersal longline (IUU; Fig. 4.2; Appendix B.3 Table B.2). As the Japanese pelagic longline fleet south of 30°S introduced voluntary bycatch mitigation measures in the late 1980s and early 1990s, we assumed that this resulted in a bycatch reduction of 20% after 1992 (Tuck et al. 2015). The estimated parameter values were insensitive to this choice. However, allowing a separate bycatch catchability to be estimated for the Japanese pelagic fleet, this did not significantly improve the model (likelihood ratio test, df = 1, p = 0.7, difference

between log likelihoods = 0.14). Therefore, the same parameter value was used for the Japanese and all other pelagic longline fleets. When the available effort data ended before 2011, the effort for the last year of data was repeated for each year through 2011, with the exception of fleets known or suspected to be inactive, in which case effort was set at zero.

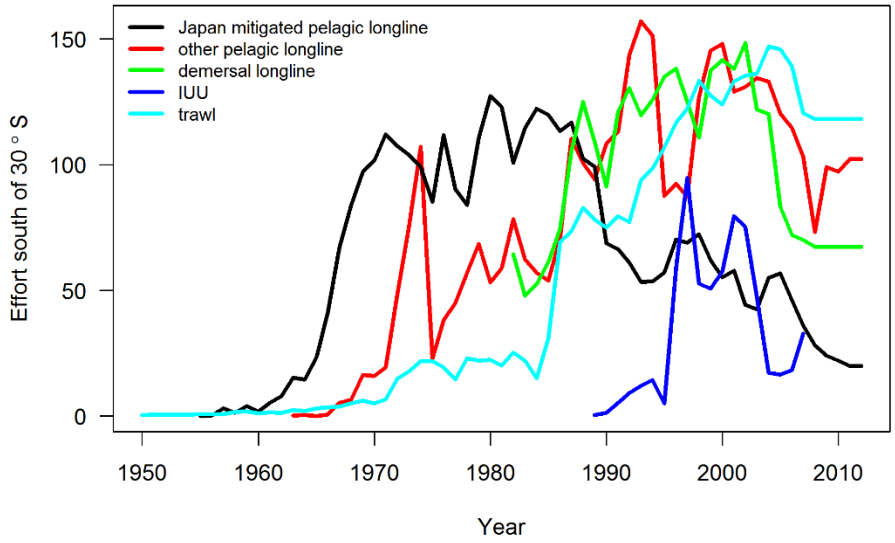

Figure 4.2: *Annual estimated magnitude of effort (million hooks or thousand trawl hours) south of 30°S by super-fleet. Effort estimates include the last year of available data repeated until 2011, excluding fleets assumed to be inactive (i.e. IUU).*

4.3.1.4 Fishery bycatch data

Reported bycatch rates (longline: birds / 1,000 hooks, trawl: birds / 1,000 hrs.) were obtained from primary literature and reports (summarized in Appendix B.4 Table B.3). As no direct observations of IUU bycatch rates are available, a single estimated value was used, which is based on bootstrapped observed bycatch rates from the legal demersal longline fleet in the same region in 1996/97 when relatively few mitigation measures were applied (Anon 2006, p. 78). To assess the sensitivity of the model estimated parameters to our assumptions regarding the IUU demersal longline super-fleet including: magnitude of effort, bycatch rate, and the

assumed probability of a BBA being caught originating from the study population, we evaluated a range of model scenarios altering our assumptions of this super-fleet (Appendix D), but do not report these in detail in the present chapter.

4.3.1.5 Environmental variables

Environmental variation could impact breeding success by altering chick mortality, as in Thomson et al. (Thomson et al., 2015; Appendix C.4). Here, four environmental co-variates were created for use as model co-variates. We assess the average SST in the (i) foraging grounds near Kerguelen during the incubation (October – December) and (ii) rearing (January – April) period, and the (iii) SST during the winter prior to breeding (May – September) in areas of broad habitat use south of Australia, as well as a relatively intense area of concentrated use (iv) northwest of Tasmania (Fig. 4.3). While environmental variation has been associated with the survival of adults (Rolland et al. 2010, Pardo et al. 2012) and inexperienced birds (Nevoux et al. 2010b), we only assess the impacts on chick mortality as the current model framework does not allow covariates on adult survival rate. The average SST across these regions for the given monthly time periods was calculated using NOAA ¼° monthly optimum interpolation dataset (Reynolds et al., 2008).

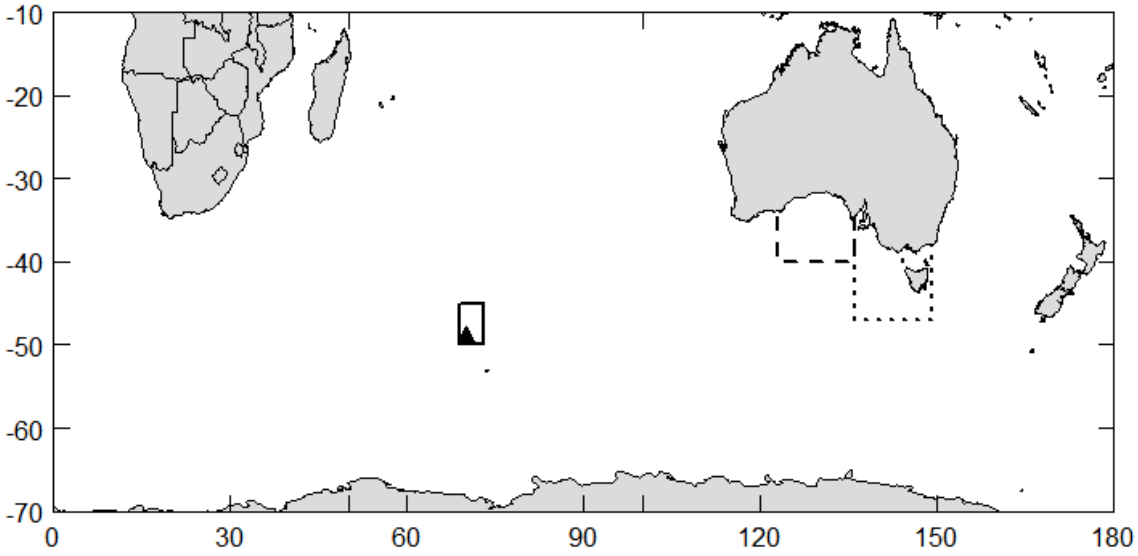

Figure 4.3*: Location of black-browed albatross breeding colony on Kerguelen, at (triangle) Cañon des Sourcils Noirs. The at-sea area defining average SST during the (solid lines) incubation and rearing period and wintering period (dashed lines) south of Australia and (dotted lines) northwest of Tasmania are shown.*

4.3.2 Population model

We apply a seabird population model based on an integrated modeling framework to assess the impacts of bycatch and the environment on albatross population demographics. Key aspects of this framework are introduced in earlier studies (Tuck, 2004; Tuck et al., 2001) and have been significantly developed through recent applications (Thomson et al., 2015; Tuck et al., 2015). The model applied in this paper is structured by sex, age-class, breeding stage, and reproductive history and operates on a monthly temporal and 5˚ × 5˚ spatial scale. Age-classes include chicks (from eggs to pre-fledging), juveniles (from departure from the colony to the end of that model year), immatures (from the start of the model year after fledging to < 5 years), and adult (5 – 70 years). We use this model to estimate demographic parameters for the virgin (un-impacted by bycatch) focal population, susceptibility to bycatch by different super-fleets, and environmental influences on chick mortality using a likelihood approach (see Appendix C for details).

Briefly, distribution at sea data are combined with fishing effort data to calculate the degree of overlap and the vulnerability to fisheries bycatch, considering the probability that a given bycatch report involved a bird from the focal population (e.g. population multiplier) and an estimated bycatch catchability parameter for each fleet. As allowing a separate bycatch catchability to be estimated for the Japanese mitigated pelagic longline fleet south of 30° S did not significantly improve the model (likelihood ratio test approximated by a chi-square test, df = 1, p = 0.29), the same parameter value was used for all pelagic longline fleets. As successfully fledging a chick typically requires provisioning from both parents (Tickell, 1968), we assume that the death of either partner would result in the death of a chick, i.e. breeding failure. Therefore, in a given model year, a breeding bird can become a failed breeder due to the loss of a partner through natural or bycatch related mortality, or the death of their chick through natural chick mortality. This change is reflected in the number of failed breeders in the following month. This is also true of age-specific mortality rates, which are density-dependent for chicks and juveniles / immatures (Appendix C.3-C.4) and all but chicks (from egg to pre-fledging) are directly susceptible to bycatch. At the start of each model year, birds are re-allocated to breeding or non-breeding status, as appropriate, and one year is added to each bird's age. The change in a given bird's age might be reflected in a change of category (e.g. juvenile to immature, immature to adult) when appropriate. Note that chicks move to the juvenile category less than a full year after hatching, at the end of the breeding season when they fledge and become vulnerable to bycatch as juveniles.

4.3.3 Selecting environmental covariates

To identify which of the four environmental co-variates we developed (see above: 'environmental variables') was most influential on chick mortality, we tested all combinations of

up to two environmental variables at a time within a fitted model and selected the best model using the likelihood ratio test, assessed at a significance level of 0.05. We did not test all combinations with three or four environmental variables as collinearity between these variables resulted in redundant information and prevented tuning of parameter values.

4.3.4 Assessing and distinguishing between parameter estimates

To assess the model's ability to precisely estimate parameter values, standard errors for parameter estimates were approximated using the inverse of the Hessian matrix evaluated at the maximum likelihood. This essentially provides a covariance matrix of values for each estimated parameter, where values indicate the correlation between parameters, thus the relative confidence in the estimated values for each of the pair of parameters, in isolation. The hessian matrix was estimated using the 'hess' function in the numDeriv R package (Gilbert and Varadhan, 2015).

Due to high correlation between several parameters and that for adult mortality, this parameter was set at the theoretical adult mortality rate assuming no impact of fisheries bycatch (i.e. virgin population), $M = 0.039$, and is therefore smaller than the mean adult mortality observed in the field. This value is similar to breeding Westland petrels (0.035), which likely have low fisheries bycatch mortality at this stage (Waugh et al., 2015) and the estimate made using the model applied in the current study for shy albatross (0.041; Thomson et al., 2015).

4.4 Results

4.4.1 Environmental covariate selection

The model producing the best agreement with demographic values included a negative relationship of the average SST around Kerguelen during incubation with chick mortality (e.g. positive relationship with chick survival; Table 4.1).

***Table 4.1**. Summary of models tuned using different combinations of environmental ('environ.') variables and their significance as compared to the null model. DF = degrees of freedom. negLL = negative log likelihood. The 'null' model includes no environmental variables. The smaller the negative log likelihood, the stronger the model. I = average SST around Kerguelen (Fig. 4.3) during incubation (October-December), R = average SST around Kerguelen during rearing (January – April), G and T are the average SST values for the boxes south of Australia and northwest of Tasmania, respectively, during the winter (May – October) prior to the breeding season. The p-values are determined by a chi-square test. **Bold** text indicates the selected model, which is significant at 0.05 despite a larger number of parameters.*

model name	variable	estimated slope	DF	negLL	negLL model - negLL null	p-value
null	none	na	0	299.03	na	na
Ix	**I**	**-0.505**	**1**	**294.72**	**4.31**	**0.04**
Rx	R	-0.168	1	298.58	0.45	0.50
Gx	G	0.311	1	298.09	0.94	0.33
Tx	T	0.432	1	296.54	2.49	0.11
IT	I T	-0.439 0.277	2	293.86	5.17	0.08
IG	I G	-0.486 0.130	2	294.55	4.48	0.11
IR	I R	-0.511 0.000	2	294.69	4.34	0.11
TG	T G	0.437 0.000	2	296.51	2.52	0.28
TR	T R	0.429 -0.152	2	296.14	2.89	0.24
GR	G R	0.329 -0.185	2	297.53	1.50	0.47

4.4.2 Model fit

The Ix model estimates fit reasonably well with the observed data and improved the estimated breeding success and juvenile survival compared to the null model (Fig. 4.4b, c). The decrease in the number of breeding pairs from the late 1990s to the mid-2000s, as well as the increase from the mid-2000s to the end of the time series is captured by the model (Fig. 4.4a). One very low value for breeding pairs in 2007 was not reproduced by the model. The sharp decrease modelled in the early 1980s relates to a very low rate of return to the colony for that year (not shown) which itself corresponds to low juvenile survival 5 years prior (Fig. 4.4c). While the large number of individuals fledged in the 1990's is not captured by the model, agreement with the observed data improves from 2000 onward (Fig. 4.4b). The increase in the average survival rate to age 5 is represented by the model, but the modelled rate remains lower than observed survival rates (Fig. 4.4c.). The sharp decline after 2001 relates to the temporal lag required to estimate survival of each cohort and does not reflect a predicted decline in juvenile survival. The range of variability in adult survival in the first years these data were estimated; the early 1980s, is not captured by the model, the decline from the 1990s to early 2000s and subsequent increase is well represented by the model (Fig. 4.4d).

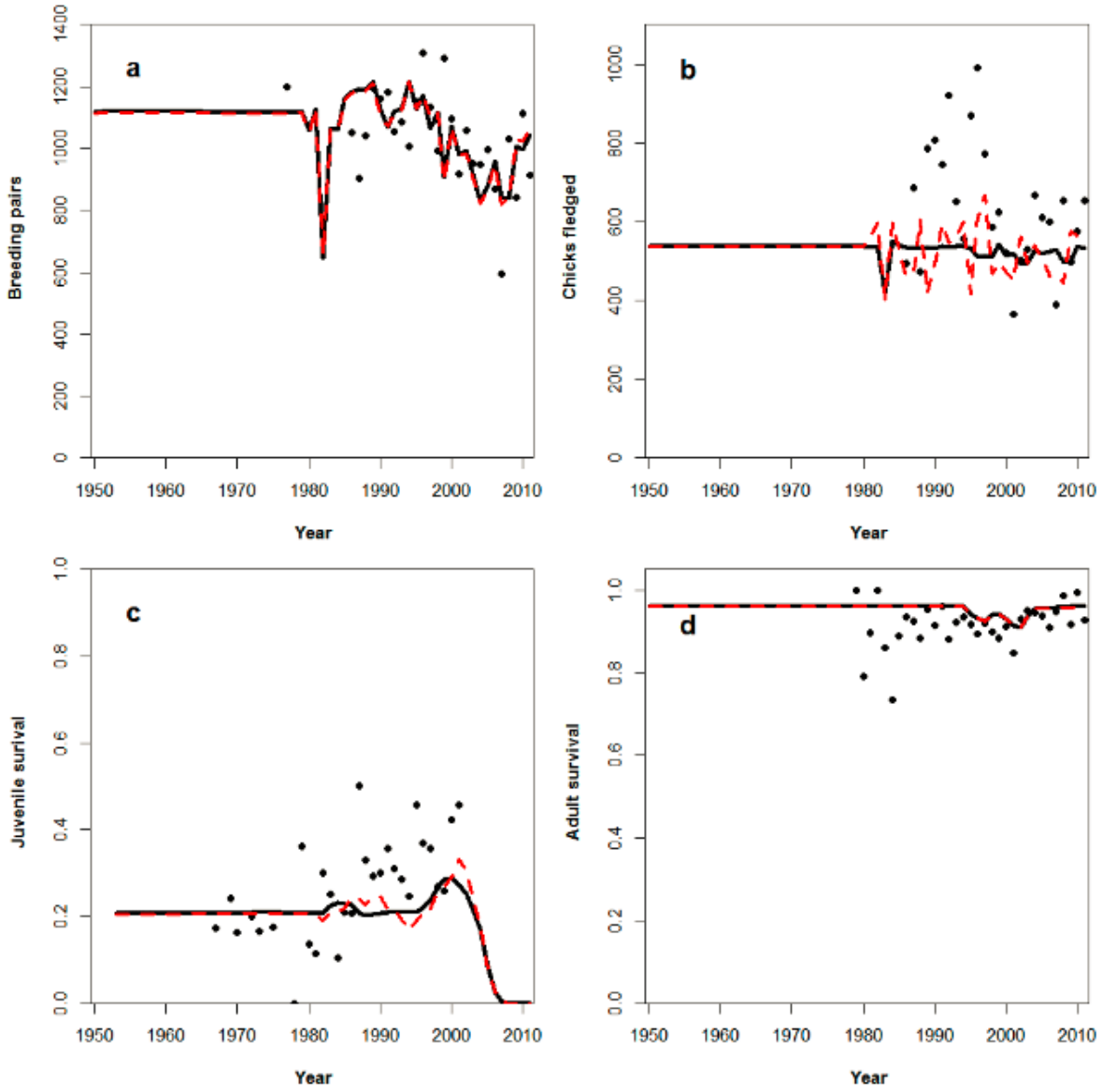

Figure 4.4: *Time series of (circles) observed and (lines) modelled (a) number of breeding pairs (b) number of chicks fledged (c) average survival to age 5, and (d), adult survival expressed as a percent, for the (black solid) null and (red dash) best (Ix) models.*

4.4.3 Parameter estimation

Including the impact of average SST around Kerguelen during the incubation period on chick mortality resulted in changes to the estimates for other parameter values. Specifically, the negative estimated slope of this covariate, which was excluded or assumed to be 0 in the null model, indicates chick mortality is reduced, thus greater chick survival, when the average SST is

relatively warm. The Ix model estimates a greater impact of density-dependence on juvenile and immature than the null model (Table 4.2). Both models indicate that the population is rebounding from lower numbers in the 1990s and is approaching or at its theoretical equilibrium number of breeding pairs, ~ 1,120 (Table 4.2). All pelagic longline effort was given the same bycatch catchability parameter ($3.58e^{-10}$), regardless of the model while legal demersal longline bycatch catchability is greater than pelagic in both models, with $1.48e^{-9}$ in the null model, which increased slightly in the Ix model at 2.10^{-9}. IUU is estimated to be a factor greater than legal demersal effort, but similar between models. Trawl bycatch catchability was similar in both models, but should not be directly compared to longline rates, as the rate units differ (number of hooks vs. number of hours). Chick mortality and the impact of density-dependence is greater in the null than Ix model (0.730 and 0.616, respectively) while productivity is very similar. Adult mortality had been fixed prior to estimating the full model.

Table 4.2. *Final parameter estimates for the selected model, Ix. Mj/i = juvenile and immature mortality rate including density-dependence (which is the same value), # BP = number of breeding pairs, Jpll = Japanese mitigated pelagic longline super-fleet bycatch south of 30˚ S rate, pll = other pelagic longline super-fleet bycatch catchability, demll = demersal longline super-fleet bycatch catchability, IUU = illegal, unreported and unregulated super-fleet bycatch catchability, trawl = trawl super-fleet bycatch catchability, Mchick = chick mortality rate including density-dependence, prod = productivity of the albatross population, SSTinc. = slope of the relationship between the average SST near Kerguelen during the incubation period and chick mortality. Madult = adult mortality. '*' indicates that the parameter value was fixed.*

parameter	**estimate**	
	null	**Ix**
Mj/i	8.62	10.69
# BP	1118	1115
Jpll	3.58E-10	3.58E-10
pll	3.58E-10	3.58E-10
demll	1.48E-09	2.10E-09
IUU	1.62E-08	1.60E-08
trawl	8.43E-08	8.46E-08
Mchick	0.730	0.616
prod	0.565	0.562
SSTinc	-	-0.505
*Madult	0.039	0.039

4.4.4 Bycatch

The majority of the estimated BBA bycatch is allocated to the IUU demersal longline super-fleet from the mid-1990s through the early 2000s, with peaks in 1997 and 2001 (Fig. 4.5). Although bycatch was estimated to occur for all fleets, the number of estimated birds is small relative to IUU.

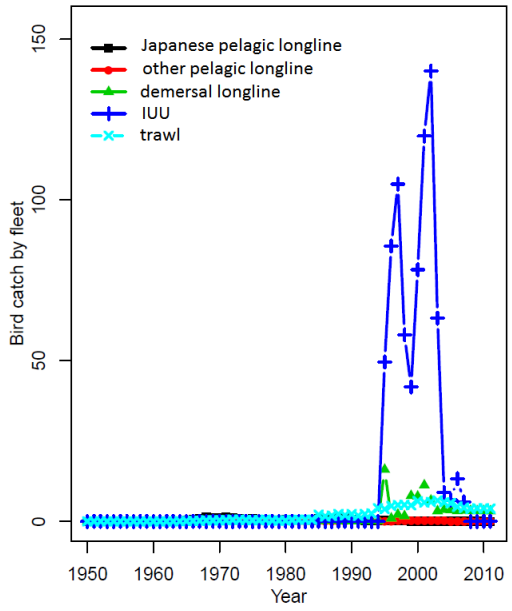

Figure 4.5*. The annual number of birds estimated to be caught as bycatch by each super-fleet.*

The presence of IUU demersal longline effort coincides with the period of modelled bycatch (Fig. 4.5, 4.6) and all modelled bycatches occurred near the breeding colony (Fig. 4.7).

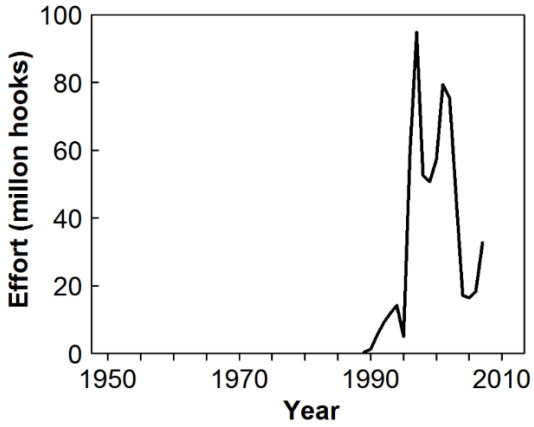

Figure 4.6. *The annual magnitude of effort (million hooks) of IUU demersal longline effort.*

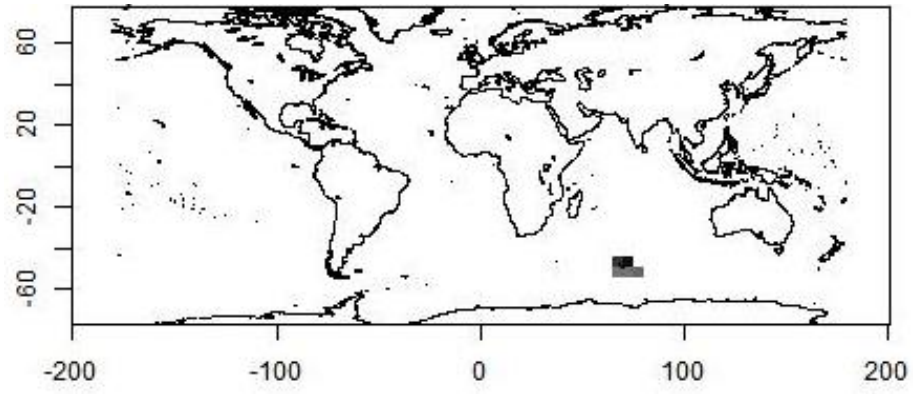

Figure 4.7*. The relative distribution of BBA bycatches attributed to the IUU demersal longline fleet.*

4.4.5 Assessment of parameter estimates

In assessing the covariance between estimated parameter values, we found a high degree of independence between most pairs of parameters, with moderate covariance between legal and illegal demersal longline effort (Fig. 4.8).

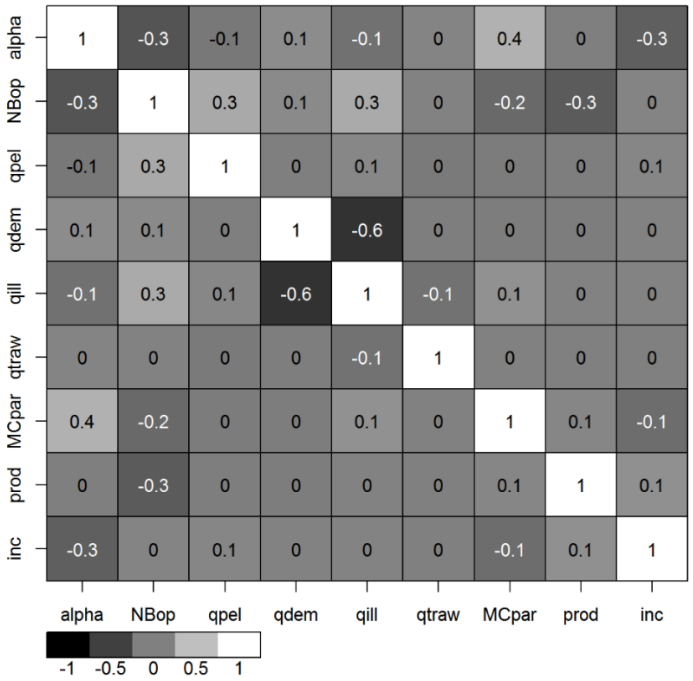

Figure 4.8*. Inverse Hessian matrix evaluated at the maximum likelihood for model tuned parameters. Values indicate covariance between estimated parameter values. Large values indicate low confidence in the model's ability to attribute a change in the population to either member of the pair of parameters. Parameter names are the same as described in Table 4.2.*

Agreement between the model estimated and observed bycatch rate varies between super-fleets (Fig. 4.9). Specifically, non-Japanese pelagic and demersal longline effort have strong agreement between observed and estimated values, with a slight tendency to over-estimate bycatch, while the agreement of Japanese and trawl effort is moderate, with a tendency to underestimate bycatch rates. Agreement with the single IUU demersal longline rate is poor with the model estimating a much lower bycatch rate. The scenarios assessing the impact of the assumptions of the IUU demersal longline super-fleet data indicate that the model performs best (lowest negative log likelihood) when the IUU estimates are included and the estimated bycatch rate of the IUU super-fleet is proportionally consistent (Appendix D, Table D.1).

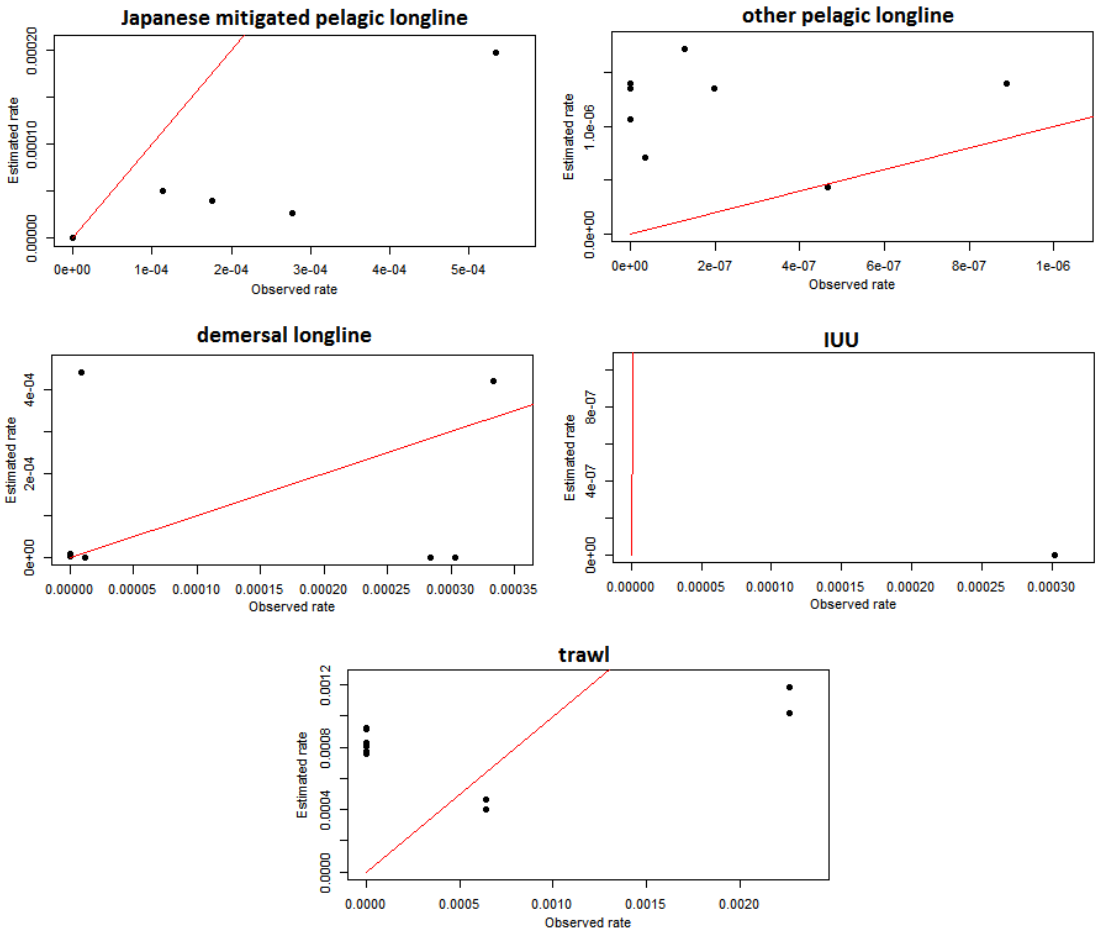

Figure 4.9. *The (x-axis) observed and (y-axis) estimated bycatch rates by super-fleet. Red line indicates a 1:1 relationship between observed and predicted bycatch. Bycatch rates are calculated as: reported bycatch * probability caught bird originated from the focal colony (population multiplier). When the right-side of this line exits the plot above (below) the upper-right corner, this indicates an average tendency to underestimate (overestimate) bycatch.*

4.5 Discussion

This study is one of few quantifying the impact of the environment, fisheries bycatch, and density-dependence using an integrated framework (Francis and Sagar, 2012; Thomson et al., 2015). These results suggest that bycatch by the IUU demersal longline fleet has had a stronger impact on historical BBA demographics than regional SST. Specifically, the observed decline in BBA on Kerguelen is related to IUU demersal longline activity. As others have also found, warmer conditions in the breeding period promote BBA population growth (Rolland et al., 2008;

Rolland et al., 2010). However, this had a lesser effect on the historic population than bycatch by the IUU fleet. Covariance among parameter estimates is low, indicating high confidence in most parameter values. By characterizing the relative impact of different factors on albatross demographics, this approach enhances the understanding and ability to manage albatross populations.

4.5.1 Inclusion of environmental variables

Despite different analytical approaches, our finding regarding the positive impact of warm conditions near the colony during the breeding period agrees with recent work on this colony (Rolland et al., 2008; Rolland et al., 2009b; Rolland et al., 2010). The impact of including SST is seen in the reduced chick mortality in the Ix versus null model (Table 4.2) and the improved estimates of the number of chicks fledged and juvenile survival (Fig. 4.4b, c). Specifically, the stronger impact of juvenile and immature mortality including density-dependence estimated by the Ix model than the null model likely reflects the strong role that natal conditions can have on juvenile survival (Fay et al., 2015; Nevoux et al., 2007). The mechanism for the slight increase in demersal longline bycatch catchability estimated in the Ix model is unclear and may be a non-significant outcome of model tuning. Overall, including pertinent environmental information provides ecological context for explaining demographic variation.

4.5.2 Impacts of the IUU fleet

The pronounced underestimate of the single estimate of IUU bycatch rate (Fig. 4.9) is important to consider when considering the implications of the model results, particularly given the significant bycatch allocated to this fleet. As the single 'observed' IUU bycatch rate was not observed in the IUU fleet but estimated from the legal fleet operating with very little mitigation

(Anonymous, 2006), it is unclear if the model estimated bycatch rate is more or less realistic than the observed rate. Furthermore, the co-variation between the parameter estimates for IUU and legal demersal effort is not surprising, given their common origin.

Despite the issues surrounding the estimation of IUU bycatch rates, multiple lines of evidence support the model findings. Specifically, the estimated bycatch rates tended to agree with that observed for the other fleets. The weaker agreement of estimated Japanese pelagic longline and trawl effort could relate to inaccurate population multiplier estimates, as comprehensive distribution at-sea data were not available. Given the general agreement with the bycatch rates of other fleets (Fig. 4.9), the temporal coincidence of IUU effort and the observed decrease in the number of breeding pairs as well as the spatial distribution of bycatch centering on the breeding colony (Fig. 4.4a, Fig. 4.5-4.7), IUU demersal effort is highly likely to have played an important role in the decline of the Kerguelen BBA population. This allocation of the majority of bycatch to the IUU fleet is robust to changes in its assumed magnitude of effort, observed bycatch rate, and the probability that a caught BBA originated from the Kerguelen colony (Appendix D).

4.5.3 Improving model agreement

Agreement between the observed and modelled demographic parameters could be increased by incorporating additional factors. Explicitly modeling cohort effects implicating natal environmental conditions (Fay et al., 2015; Nevoux et al., 2007) or parental age (Fay et al., 2016) could improve the estimates of juvenile survival to age 5. Incorporating a parameter to represent increased survival as a result of supplemental feeding on trawl offal (Rolland et al., 2008; Rolland et al., 2010) could improve the estimate of the number of chicks fledged.

Incorporating the impact of the environment on the survival of additional age-classes into the model framework could improve mortality estimates (Rolland et al. 2010, Pardo et al. 2012). Lastly, the variability in adult survival in the early portion of the study period is related to relatively low sample sizes in the early years of data collection, therefore high standard error, associated with these parameter estimates. This variability could also relate to variability in the temporal extent of fishing data available (Appendix B.3, Table B.2), or higher adult mortality associated with higher pre-mitigation bycatch rates.

4.5.4 The future of the Kerguelen BBA population

Currently, the BBA population on Kerguelen appears to have rebounded from relatively low population size and is near to its theoretical (and observed) maximum number of breeding pairs. The recent absence of IUU longline effort, continued international pressures to eliminate IUU (FAO, 2016), and the relatively low bycatch rates estimated for other fleets, suggest this population could remain stable around the current number of breeding pairs. Furthermore, the continued projected increase in SST (IPCC, 2013) could promote chick survival, potentially leading to density-dependent factors dominating chick and juvenile mortality. However, the relationship with SST may be non-linear (Barbraud et al., 2011), such that too much warming will lead to a decline, presenting alternate trajectories depending on the full functional relationship of SST and chick survival (Thomson et al., 2015).

An important unknown in this system is the future distribution of fishing effort by the fleets in this region. While studies have projected shifts in tuna distributions (Dueri et al., 2014; Lehodey et al., 2015; Lehodey et al., 2010), including poleward shifts for temperate species (Dell et al., 2015; Hobday, 2010), the distribution of fishing effort is ultimately determined by the fishers and their response will likely depend on multiple factors, including perceived risk

(Dowling et al., 2013). Although bycatch was modelled as relatively low in the legal fleets, shifts in the distribution and timing of effort could result in different bycatch patterns developing. Recent studies finding that economic incentives could be used to reduce bycatch in some fleets (Mangel et al., 2015; Pascoe et al., 2013) offer new insights into the potential applications of fleet dynamic models and the estimation of future bycatch risk.

Attributing bycatch to different super-fleet and the relative impacts of environmental conditions on population dynamics provides novel insight into the factors driving albatross population dynamics. The integrated approach demonstrated here and elsewhere (Francis and Sagar, 2012; Thomson et al., 2015; Tuck et al., 2015) allows the quantification of the impact of each factor and the resulting estimates are readily interpreted and assessed for covariance. Such an approach can be used to inform managers of key interactions, direct the design of critical experiments by scientists, and identify data gaps (e.g. IUU bycatch estimates).

4.6 Acknowledgements

We are particularly grateful to all the field workers involved in the monitoring program over the past 40 years on the black-browed albatross at Cañon des Sourcils Noirs, Kerguelen Island. The present work was supported financially and logistically by the Institut Polaire Français Paul Emile Victor (program 109), Terres Australes et Antarctiques Françaises, Zone Atelier de Recherches sur l'Environnement Antarctique et Subantarctique (CNRS-INEE), and has been approved by the ethics committee of IPEV and by the Comité de l'Environnement Polaire . We also thank Sophie Jeudi de Grissac and Henri Weimerskirch (CNRS-CEBC) for sharing and providing guidance on the use juvenile albatross distribution at-sea data. We thank D. Besson for the data management. We thank all of the organizations and individuals whom

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Appendix B Additional information on data in used in the albatross population dynamics model

B.1 Monthly at-sea distributions by albatross category

Table B.1 *Distinct distribution at-sea patterns allocated each month to each category of albatross: currently breeding adults, adults failed breeding in the current season, non-breeding adults who failed the previous season, non-breeding adults who were successful the previous season, juveniles (fledged the current year), and immature birds (age >1 – 5). "*" indicates males and females are modelled separately for the specified category. No juveniles are present at-sea until they fledge and migrate from the colony. Note that the model year begins in October, the beginning of the breeding season for black-browed albatross at the focal colony at Cañon des Sourcils Noirs, Kerguelen Island.*

Month	Adult, breeding	Adult, failed breeding	Adult, non-breeding: previously failed*	Adult, non-breeding: previously successful*	Juvenile	Immature
Oct	incubating	resident	resident	resident	-	independent
Nov	incubating	resident	resident	resident	-	independent
Dec	incubating	resident	resident	resident	-	independent
Jan	rearing	resident	resident	resident	-	independent
Feb	rearing	migrating	migrating	migrating	-	independent
Mar	rearing	migrating	migrating	migrating	-	independent
April	rearing	wintering	wintering	wintering	migrating	independent
June	wintering	wintering	wintering	wintering	wintering	independent
July	wintering	wintering	wintering	wintering	wintering	independent
Aug	wintering	wintering	wintering	wintering	wintering	independent
Sept	wintering	wintering	wintering	wintering	wintering	independent

B.2 Description of the refinements to the effort data for IOTC longline fleets

4.6.1 Context

Longline fisheries supply the majority of high value, sashimi-grade tuna represent a significant proportion of tuna catch, value (Hamilton et al., 2011). However, the magnitude, distribution, and the fleets allocating effort have fluctuated over time. Commercial distant-water pelagic fishing vessels, often targeting tunas and tuna-like species, began in the 1950s, starting

with the Japanese fleet (Moreno and Herrera, 2013). The number of commercial longline fleets and the magnitude of effort rapidly increased over the next few decades following decades. In the 1970s to mid-1980s, increasing fuel prices, changes in market demand, technological developments, and declarations of Exclusive Economic Zones altered the general trend of increasing and expanding effort for some fleets (Caton and Ward, 1996). Increasing concern over the distribution and management of tuna catches as well as illegal, unreported, and unregulated (IUU) fishing resulted in the development of multi-nation Regional Fisheries Management Organizations (RFMOs), which play an important role in the governance of international fisheries. The magnitude and distribution of effort by various fleets has also changed in response to a reduction of species-specific catch limits (Chen, 2012; Tuck et al., 2003). Additionally, previous and current efforts by multiple RFMOs to limit fishing capacity (Aranda et al., 2012; Joseph et al., 2010; Moreno and Herrera, 2013) have likely altered the distribution of effort (Michael et al., 2015; Tuck et al., 2003).

Fishing effort in the Indian Ocean has region-specific dynamics. Firstly, the Indian Ocean as a whole has a much greater semi-industrial component than the Atlantic or Pacific; a component which is poorly understood, as many Indian Ocean Tuna Commission (IOTC) resolutions do not include vessels in this category (Moreno and Herrera, 2013). Furthermore, piracy from Somalia impacted the tuna fishery in recent years (2009-2011), where multiple fleets displaced effort to other areas in the Indian Ocean or to other oceans (Moreno and Herrera, 2013).

The southern (south of 20° S) Indian Ocean is likely less impacted by the semi-industrial fleet and piracy than more northern regions. The magnitude of longline effort is higher than the southern Atlantic, with the Taiwanese fleet expending greater effort than the Japanese (Michael

et al., 2015). As more fleets provide effort data, additional insights into the dynamic nature of effort into this region are gained, including potential interactions with bycatch species (Barbraud et al., 2013; Tuck et al., 2015). However, as more information is obtained, the estimates of catch and effort based on these data can change slightly over time, with the most recent estimates based on more information.

The purpose of this appendix is to provide the methods for the updated estimates of the distribution and magnitude of longline effort in the southern Indian Ocean used in Ch. 4, Ch. 5 (below), and shared with individuals mentioned in the front matter. The fleets estimated include: deep-freezing pelagic longline effort for Taiwan, Korea, Seychelles, Spain, Reunion, China, and Taiwanese fresh longline. Japanese effort also evaluated, although the effort estimates are not altered from those provided.

4.6.2 Methods

Nominal (yearly aggregate catch and effort) and logbook (monthly catch and effort by fishing cell) were retrieved from the IOTC website: http://www.iotc.org/data/datasets on 2013 April 3. It is often the case that the annual catch data is not equal, generally larger, to the sum of the monthly logbook catch data. To obtain a more accurate estimate of effort, the number of hooks in the monthly logbook data were raised by the ratio of reported yearly catch to the annual sum of monthly logbook catch (Campbell, 2003).

When both nominal and logbook data were present and fish weight was provided in logbook data, effort (number of hooks) data were regionally raised based on the ratio of the nominal to logbook catch for each year. This ratio is called the 'raising factor'. The species used in this calculation were yellowfin tuna, blue-eye tuna, albacore tuna, swordfish, and

southern bluefin tuna. When nominal data were provided but logbook data were provided without weights, the number of unraised hooks was estimated. This was done by multiplying the number of nominal hooks in the nearest following year with catch logbook catch weight by the ratio of catch weight of the five species mentioned above in the year in question to that of the nearest year.

To calculate the raised effort when logbook data were not provided or provided without species weights, the regional annually weighted raising factor (RAWRF) was used to estimate the number of hooks. The RAWRF is calculated as follows:

$$R_{ri} = (8/15^*)\, R_{ri+1} + (4/15)^*\, R_{ri+2} + (2/15)^*\, R_{ri+3} + (1/15)^*\, R_{ri+4}$$

where R is the raising factor in a given region *r* (usually east or west), in a given year *i*.

If the raising factor for any of the four following years was not available, the raising factor for the year directly following was used. For years with nominal data before logbook data were provided, raised effort was calculated as follows:

$$\textit{Raised effort}_{ri} = R_{ri} * (\textit{Nominal catch weight}_{riJ} / \textit{Nominal catch weight}_{ri}) * \textit{number of unraised hooks}_{rij,}$$

where *r* is a given region, *i* is a given year, and *ij* is the most recent adjacent year.

The spatial distribution of effort for years with nominal but without logbook data was assigned by averaging the percent effort per 5° x 5° cell from the following and (when available) preceding year. Spatial distribution for years preceding logbook data was assigned for the Chinese Deep-freezing longline fleet from 1995-1998 and Taiwanese Fresh longline fleet, for 2001-2006. The distribution of effort (percent of annual effort) was assumed as the average of 1999 and 2000 for China and from 2007 for the Taiwanese fresh longline fleet. For the Taiwanese fresh longline fleet, only 2007 was used as a precaution relating to decreasing

reliability of data from relatively recent years (e.g. 2008), as information on these years may still be coming available to the IOTC.

As Japanese Nominal and logbook data describe catch in different units (weight and number of fish, respectively), and the average weight of tunas are likely to vary in space and time, we were unable to estimate effort for this fleet. Of the fleets evaluated, the data for the Korean fleet presented the most challenges to estimating effort and inspired the development of many of the above methods. Effort data are updated frequently and past effort estimates of effort can change as more information becomes available. Therefore, performing the above methods on the currently available data from the IOTC website is likely to yield slightly different estimates of total effort from those below.

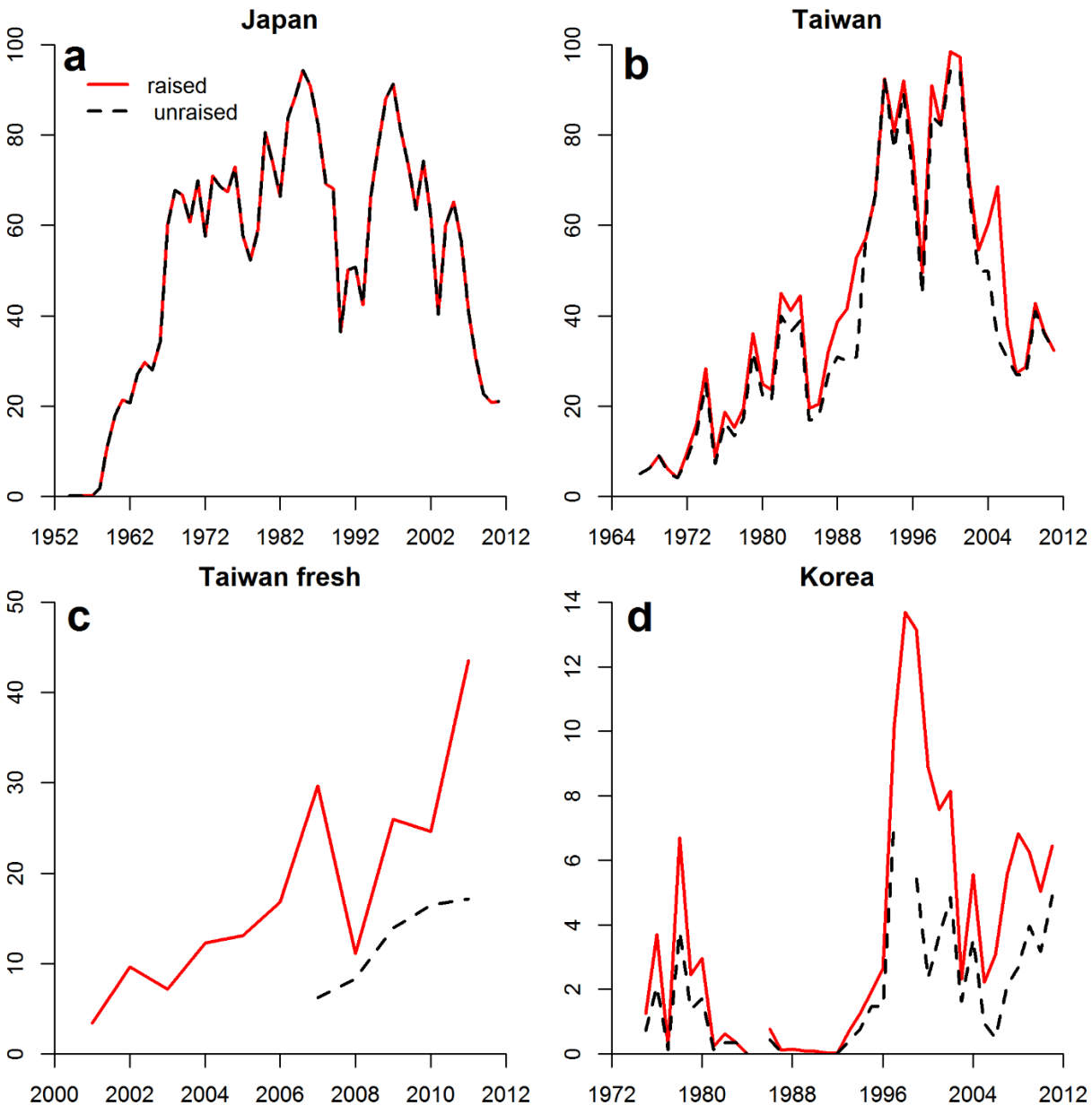

Figure B.1 *Annual sum of effort (million hooks) for the (a) Japanese, (b) Taiwanese, (c)Taiwanese fresh, and (d) Korean distant water longline fleets south of 20° S in the Indian Ocean from (black dashed) unraised and (red solid) raised data, downloaded from the IOTC website on 3 April 2013. No data were remove. Taiwanese effort (b) before 1967 are not shown because of a discrepancy between logbook (1967 -2011) and nominal (1954-2011) data ranges.*

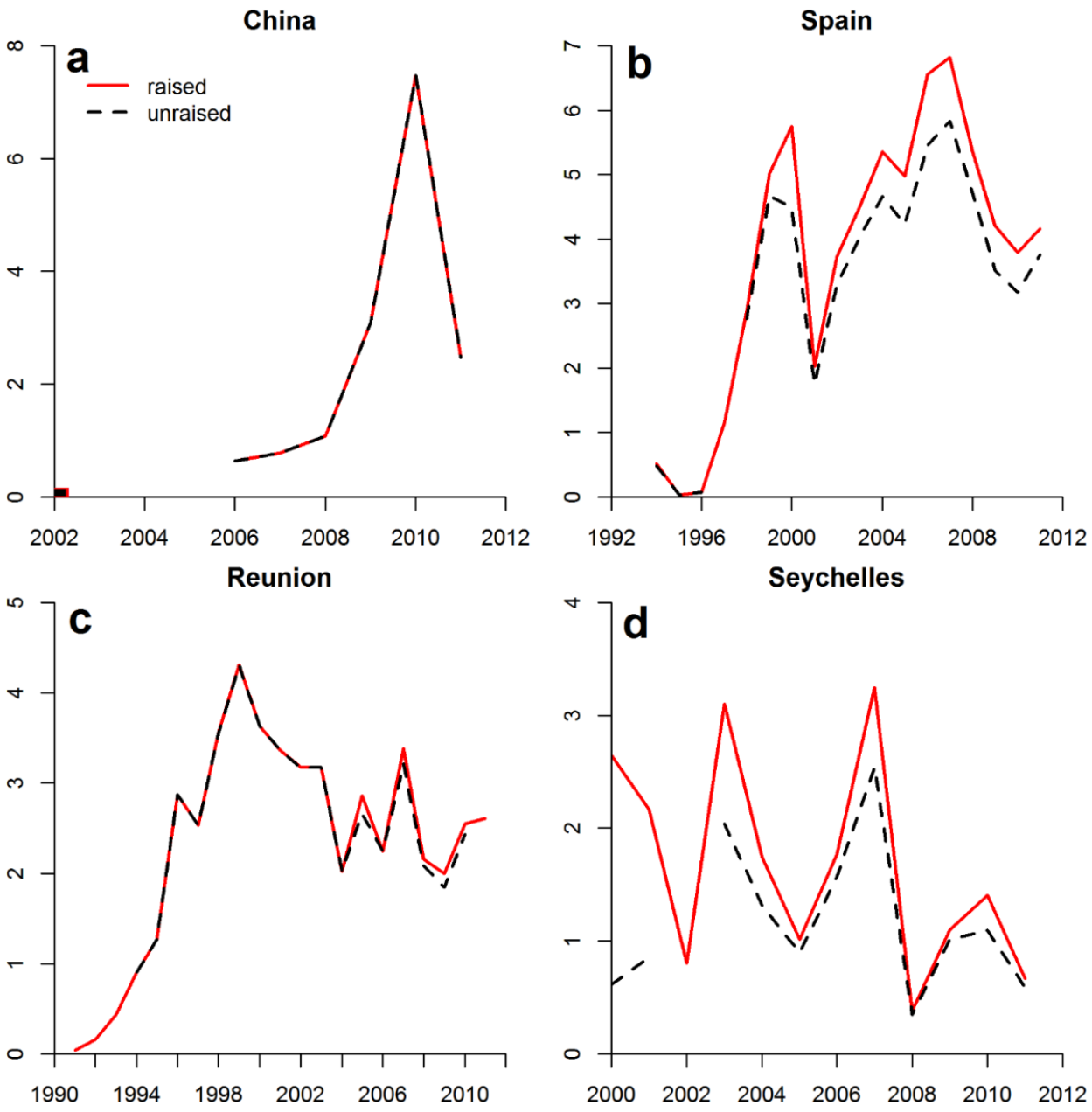

Figure B.2 *Annual sum of effort (million hooks) for the (a) Chinese, (b), Spanish , (c) Reunionese, and (d) Seychellois distant water longline fleets south of 20° S in the Indian Ocean from (black dashed) unraised and (red solid) raised data, downloaded from the IOTC website on 3 April 2013. The Seychellois effort data (d) do not start before 2000.*

B.3 Summary of fleets used in model

Table B.2 *Summary of the fleets included in the model, the associated super-fleet, temporal range of data, the average magnitude and standard error (SE) of effort. Effort is number of hooks (longline; "LL") or hours trawling (trawl). Super-fleets include: Japanese mitigated pelagic longline south of 30˚ S ("Jap Pel LL"), other pelagic longline fleets ("Pel LL"), demersal longline ("Dem LL"), illegal, unreported, and unregulated (IUU) demersal longline in Committee for the Conservation of Antarctic Living Marine Resources waters ("IUU Dem LL"), and "Trawl". IOTC = Indian Ocean Tuna Commission, ICCAT = International Commission for the Conservation of Atlantic Tunas, SPC = Secretariat of the Pacific Community, ETBF = eastern tuna and billfish, WA = Western Australia., combined, names following ";" indicate target species, SWO = swordfish targeting, nonSWO = non-swordfish targeting. '*' indicates fleets who's effort is assumed to be 0 after the last year of data.*

Fleet	Super-fleet	1st year	last year	Avg. mag. of effort	SE effort
Argentina; Hake, Ling	Dem LL	1992	2007	120,083	8,313
Argentina; Toothfish	Dem LL	1992	2007	60,053	2,686
Australia	Dem LL	1997	2006	121,660	6,658
CCAMLR legal mitigated	Dem LL	1985	2006	316,136	29,784
Chile; Hake, Ling	Dem LL	1982	2006	5,568,666	326,556
*Chile; Toothfish	Dem LL	1991	2005	1859293	81,108
Falkland within EEZ	Dem LL	1992	2008	12,504	64
Falkland outside of EEZ	Dem LL	1997	2008	12,085	124
Namib	Dem LL	1997	2006	17312	42
NZ	Dem LL	1991	2006	42789	1,053
South Africa; Hake	Dem LL	1994	2004	55,331	1,491
*South Africa; Kingklip	Dem LL	1983	1990	226,548	10,587
*CCAMLR IUU	IUU Dem	1989	2007	86944	2,700
ICCAT Japan south of 30S	Jap Pel LL	1961	2007	111,180	5,044
IOTC Japan south of 30S	Jap Pel LL	1952	2011	81,574	924
SPC Japan south of 30S	Jap Pel LL	1952	2006	184,329	5,690
Australia ETBF; SWO	Pel LL	1987	2008	988	2
Australia WA; nonSWO	Pel LL	1986	2007	1,158	4
Australia WA; SWO	Pel LL	1989	2007	1,140	2
Chile; SWO	Pel LL	1989	2007	72,107	2,671
ICCAT Brazil; nonSWO	Pel LL	1958	2006	68,386	1,591
ICCAT Brazil; SWO	Pel LL	1961	2007	8,918	225
ICCAT China	Pel LL	1993	2006	174,183	7,128
ICCAT Cuba	Pel LL	1959	2006	94,590	2,383

Fleet	Super-fleet	1st year	last year	Avg. mag. of effort	SE effort
ICCAT Cyprus	Pel LL	1975	2006	96744	6,415
ICCAT Greece	Pel LL	1981	2006	983,895	87,516
ICCAT Japan north of 30S	Pel LL	1956	2007	97,633	1,083
ICCAT Korea	Pel LL	1964	2007	115,151	2,321
ICCAT Mexico	Pel LL	1981	2006	31,794	1,758
ICCAT Namibia	Pel LL	1997	2006	54,758	2,955
ICCAT others fleets	Pel LL	1959	2007	23,027	196
ICCAT Panama	Pel LL	1972	2006	105,365	10,808
ICCAT South Africa; nonSWO	Pel LL	1963	2006	16,873	1,184
ICCAT South Africa; SWO	Pel LL	1998	2006	14,143	985
ICCAT Spain	Pel LL	1950	2006	178,336	3,284
ICCAT Taiwan	Pel LL	1962	2007	168,528	1,778
ICCAT Uruguay	Pel LL	1981	2007	45,991	5,623
ICCAT USA	Pel LL	1952	2006	21,887	476
ICCAT Vanuatu-Belize	Pel LL	2004	2006	109,373	8,683
ICCAT Venezuela	Pel LL	1957	2006	67,547	1,839
IOTC China	Pel LL	1995	2011	206,612	6,732
IOTC Japan north of 30S	Pel LL	1959	2011	184,571	3,419
IOTC Korea	Pel LL	1975	2011	129,443	2,300
IOTC Mauritius; nonSWO	Pel LL	1978	2006	3,607	176
IOTC Mauritius; SWO	Pel LL	2001	2006	6,178	317
IOTC Reunion	Pel LL	1991	2011	39,167	1,509
IOTC South Africa; nonSWO	Pel LL	1998	2006	10,882	896
IOTC South Africa; SWO	Pel LL	1998	2006	10,253	830
IOTC South Africa; Shark	Pel LL	2004	2006	13,222	1,402
IOTC Seychelles	Pel LL	1983	2011	42,847	1,175
IOTC Spain	Pel LL	1993	2011	61,834	3,566
IOTC Taiwan Fresh	Pel LL	2001	2011	146,208	3,871
IOTC Taiwan	Pel LL	1967	2011	244,181	2,631
Southeast Pacific Spain	Pel LL	1990	2006	84,013	5,907
SPC Australia; nonSWO	Pel LL	1985	2007	64,111	2,721
SPC Japan north of 30S	Pel LL	1950	2006	126,563	663
SPC Korea	Pel LL	1962	2007	148,976	1,674
SPC New Zealand	Pel LL	1990	2007	141,780	6,728
SPC other fleets	Pel LL	1981	2007	88,136	1,080

Fleet	Super-fleet	1st year	last year	Avg. mag. of effort	SE effort
SPC Taiwan	Pel LL	1958	2007	198,236	3,742
Argentina	Trawl	1958	2007	790	18
Australia	Trawl	1974	2008	2,998	63
Falkland	Trawl	1987	2007	1,072	32
*France, Kerguelen EEZ	Trawl	1979	1996	45	11
Namibia	Trawl	1964	2007	7,052	190
New Zealand; Hoki	Trawl	1997	2006	994	52
New Zealand; Squid	Trawl	1998	2006	4	n.a.
South Africa Offshore	Trawl	1930	2006	127	3
*Ukraine, Kerguelen EEZ	Trawl	1979	1995	269	40
Uruguay	Trawl	1950	2007	648	26

B.4 Summary of black-browed albatross bycatch rates

Table B.3 *Summary of black-browed albatross bycatch rates obtained from published and unpublished sources. Super-fleet abbreviations are as in Table B.2. Date ranges are described from the first month (Month 1) and year (Year 1) to last month (Month 2) and year (Year 2) and the area of bycatch is bounded by the four corners (Latitude South, Latitude North, Longitude West and Longitude East) of the overlapping 5˚ × 5˚ cells, given as the center point of each cell. Bycatch rates are the number of birds / 1,000 hooks (longline) or / 1,000 hours trawled (trawl). The population multiplier indicates the proportion of black-browed albatross likely to be a part of the focal population (Cañon des Sourcils Noirs, Kerguelen Island) where smaller values indicate a lower proportion of the focal population.*

Super-fleet	Month 1	Year 1	Month 2	Year 2	Latitude South	Latitude North	Longitude West	Longitude East	Bycatch	Population Multiplier	Reference
Jap Pel LL	5	1988	6	1988	-42.5	-42.5	142.5	142.5	1.29E-01	4.61E-03	(Brothers, 1991)
Jap Pel LL	4	1992	3	1993	-32.5	-47.5	112.5	152.5	2.71E-02	4.06E-03	(Klaer and Polacheck, 1997)
Jap Pel LL	4	1993	3	1994	-32.5	-47.5	112.5	152.5	6.62E-02	4.06E-03	(Klaer and Polacheck, 1997)
Jap Pel LL	4	1994	3	1995	-32.5	-47.5	112.5	152.5	4.21E-02	4.06E-03	(Klaer and Polacheck, 1997)
Jap Pel LL	1	1998	12	2005	-37.5	-32.5	17.5	27.5	2.00E-02	2.29E-05	(Petersen et al., 2009)
Pel LL	1	2002	5	2002	-32.5	-27.5	312.5	312.5	1.35E-01	2.85E-03	(Mancini et al., 2009)
Pel LL	6	2002	10	2002	-32.5	-27.5	312.5	312.5	1.10E-01	2.85E-03	(Mancini et al., 2009)
Pel LL	6	2003	10	2003	-32.5	-27.5	312.5	312.5	7.72E-02	2.85E-03	(Mancini et al., 2009)
Pel LL	10	2003	9	2004	-52.5	-27.5	162.5	187.5	6.83E-04	1.58E-04	(Abraham and Thompson, 2009)
Pel LL	6	2004	10	2004	-32.5	-27.5	312.5	312.5	2.24E-02	2.85E-03	(Mancini et al., 2009)
Pel LL	6	2005	10	2005	-32.5	-27.5	312.5	312.5	8.03E-02	2.85E-03	(Mancini et al., 2009)
Pel LL	10	2005	9	2006	-52.5	-27.5	162.5	187.5	4.71E-03	1.58E-04	(Abraham and Thompson, 2009)
Pel LL	1	2006	5	2006	-32.5	-27.5	312.5	312.5	4.54E-02	2.85E-03	(Mancini et al., 2009)
Pel LL	6	2006	10	2006	-32.5	-27.5	312.5	312.5	2.58E-01	2.85E-03	(Mancini et al., 2009)
Pel LL	10	2006	9	2007	-52.5	-27.5	162.5	187.5	1.05E-03	1.58E-04	(Abraham and Thompson, 2009)
Pel LL	1	2007	12	2007	-42.5	-32.5	7.5	32.5	2.12E-02	2.00E-05	(Ryan et al., 2009a, b)
Pel LL	1	2007	5	2007	-32.5	-27.5	312.5	312.5	8.84E-02	2.85E-03	(Mancini et al., 2009)
Pel LL	6	2007	10	2007	-32.5	-27.5	312.5	312.5	3.37E-01	2.85E-03	(Mancini et al., 2009)
Pel LL	1	2008	12	2008	-42.5	-32.5	7.5	32.5	1.58E-03	2.00E-05	(Ryan et al., 2009a, b)
Pel LL	6	2008	10	2008	-32.5	-27.5	312.5	312.5	3.77E-01	2.85E-03	(Mancini et al., 2009)
Dem LL	11	1994	4	1995	-47.5	-47.5	67.5	67.5	3.40E-02	4.33E-03	(Weimerskirch and Wilson, 2000)

Super-fleet	Month 1	Year 1	Month 2	Year 2	Latitude South	Latitude North	Longitude West	Longitude East	Bycatch	Population Multiplier	Reference
Dem LL	11	1995	4	1996	-47.5	-47.5	67.5	67.5	7.70E-02	4.33E-03	(Weimerskirch and Wilson, 2000)
Dem LL	3	1996	7	1996	-57.5	-52.5	317.5	327.5	8.15E-02	4.12E-03	(Anonymous, 1996)
Dem LL	11	1996	4	1997	-47.5	-47.5	67.5	67.5	2.00E-03	4.33E-03	(Weimerskirch and Wilson, 2000)
Dem LL	3	1997	4	1997	-57.5	-52.5	317.5	327.5	3.48E-01	4.12E-03	(Anonymous, 1997)
Dem LL	5	1997	8	1997	-57.5	-52.5	317.5	327.5	3.32E-03	4.12E-03	(Anonymous, 1997)
Dem LL	4	1998	4	1998	-57.5	-52.5	317.5	327.5	3.84E-03	4.12E-03	(Anonymous, 1998)
Dem LL	5	1999	7	1999	-57.5	-52.5	317.5	327.5	1.05E-02	4.12E-03	(Anonymous, 1999)
IUU Dem LL	9	1995	4	1996	-57.5	-52.5	317.5	327.5	3.47E-01	4.12E-03	(Anonymous, 2006)
Trawl	4	2004	9	2004	-37.5	-32.5	17.5	27.5	9.04E+01	2.29E-05	(Watkins and Ryan, 2008)
Trawl	10	2004	3	2005	-37.5	-32.5	17.5	27.5	2.57E+01	2.29E-05	(Watkins and Ryan, 2008)
Trawl	4	2005	9	2005	-37.5	-32.5	17.5	27.5	9.04E+01	2.29E-05	(Watkins and Ryan, 2008)
Trawl	10	2005	12	2005	-37.5	-32.5	17.5	27.5	2.57E+01	2.29E-05	(Watkins and Ryan, 2008)
Trawl	1	2006	12	2006	-37.5	-32.5	17.5	27.5	8.68E-06	2.29E-05	(Maree et al., 2014)
Trawl	1	2007	12	2007	-37.5	-32.5	17.5	27.5	8.68E-06	2.29E-05	(Maree et al., 2014)
Trawl	1	2008	12	2008	-37.5	-32.5	17.5	27.5	8.68E-06	2.29E-05	(Maree et al., 2014)
Trawl	1	2009	12	2009	-37.5	-32.5	17.5	27.5	8.68E-06	2.29E-05	(Maree et al., 2014)
Trawl	1	2010	12	2010	-37.5	-32.5	17.5	27.5	8.68E-06	2.29E-05	(Maree et al., 2014)
Trawl	1	2011	12	2011	-37.5	-32.5	17.5	27.5	8.68E-06	2.29E-05	(Maree et al., 2014)

B.5 Summary of the proportion of birds having bred at a given age

Table B.4 *Proportion of birds having bred at a given age. '1' indicates all birds of that age have bred at least once.*

age	proportion
1	0.00
2	0.00
3	0.00
4	0.00
5	0.01
6	0.08
7	0.23
8	0.47
9	0.63
10	0.78
11	0.86
12	0.91
13	0.94
14	0.98
15	0.99
16	1.00

Appendix C Technical description of albatross population model

The model used here is the same model used in Thomson et al. (2015), with updated fishing effort for major Indian Ocean pelagic longline fleets (see section B.2), different enviormental covariates, colony and species-specific bycatch rates and popmulti estimates. Therefore, much of the material in this appendix is very similar to the S3 Appendix in Thomson et al. (2015). The catagories for birds within the population differ slightly as well, with the addition of non-breeding individuals who previously failed breeding, non-breeding indiviuals who previously successfully breed (fledged a chick), and distinct spatial distributions for juvenile and immature birds.

C.1 Within year dynamics

As successfully fledging a chick often requires provisioning from both parents (Tickell, 1968; Warham, 1990), we assume that the death of either partner (p) would result in the death of a chick, therefore breeding failure.

The model year begins on 1 October (model month m =1) when breeding commences. The number of birds hatched at the beginning of model year y (designated as 'chicks') is given by N_y^0. Once chicks leave the colony (fledge) in April, they become'juveniles, J until the end of that model year. From the start of thier second year of life birds are termed immatures until they first recruit to the breeding colony (given by an ogive; Table B.4, starting at age 5).

The population is divided into chicks, and an additional six categories (breeding bx, failed breeders bf, non-breeding individuals who failed breeding the previous season $ns-f$, non-breeding individuals who successfully breed the previous season $ns-s$, juveniles J and

immatures I), so that the number of birds of sex *g*, and age a and in any category c during year y and month m is given by $N^{c}_{g,a,y,m}$,

$$N^{c}_{g,a,y,m} = \left[N^{bx}_{g,a,y,m}, N^{bf}_{g,a,y,m}, N^{ns-f}_{g,a,y,m}, N^{ns-s}_{g,a,y,m}, N^{J}_{g,a,y,m}, N^{I}_{g,a,y,m} \right].$$

Sex-specific at-sea distributions are used failed breeders. The model 'year' begins when birds arrive at their breeding colony (assumed to be the same day, for all birds of a given population) and ends at the end of April the following calendar year. On arrival, birds are assigned to the 'breeding' category $N^{bx}_{g,a,y,m}$ and, unless their breeding attempt fails during any month, they remain in this category until the end of the breeding season (at the end of month *Q*). Each month m, some surviving birds fail in their breeding attempt because their mate dies of natural causes (at instantaneous monthly rate $M/12$) or is caught by a fishery (at instantaneous monthly rate $F^{bx}_{g,y,m}$ for adult birds in category *c=bx*) or their chick dies (at instantaneous annual rate $M^{0}_{y}/12$). The number of surviving birds remaining in the breeding category at the start of month *m* is given by

$$N^{bx}_{g,a,y,m} = N^{bx}_{g,a,y,m-1}\, e^{-(M/12+F^{bx}_{g',y,m-1}+M^{0}_{y}/12)}\, e^{-(M/12+F^{bx}_{g,y,m-1})} \qquad m = 2 \ldots Q,$$

where g' is the sex of the mate of a bird of sex g .

Chick mortality M^{0}_{y} and adult mortality M are independent of sex and adult category, but fishing mortality $F^{c}_{g,y,m}$, because it depends on spatial overlap with fishing fleets differs between sexes *g*, and between adult (categories *bx, bf, ns-f* and *ns-s*), and pre-breeding birds (categories *J and I*) and changes monthly as at-sea distributions for fishing fleets vary.

Any breeding bird that fails in its breeding attempt during month *m-1* is moved into the failed breeders category at the start of the following month $N^{bf}_{g,a,y,m}$. The number of birds in the failed

breeder category at the start of month *m* is given by those that remain from the previous month (that survive both natural and fishing mortality), plus those (surviving) breeders whose breeding attempt failed during the previous month m *-1*,

$$N^{bf}_{g,a,y,m} = N^{bf}_{g,a,y,m-1}\, e^{-(M/12+F^{bx}_{g,y,m-1})}$$

$$+ N^{bx}_{g,a,y,m-1}\left[1-e^{-(M/12+F^{bx}_{g',y,m-1}+M^{0}_{y}/12)}\right]e^{-(M/12+F^{c}_{g,y,m-1})} \qquad m=2\ldots Q\ .$$

After the breeding season ends, all surviving breeding or failed birds move into the non-breeding category alongside surviving birds that did not attempt to breed during year *y*, reliative to their success or failure breeding the year prior,

$$\begin{aligned} N^{ns-f}_{g,a,y,Q+1} &= N^{ns-f}_{g,a,y,Q}\, e^{-(M/12+F^{ns-f}_{g,y,Q})} + N^{bx}_{g,a,y,Q}\, e^{-(M/12+F^{bx}_{g,y,Q})} + N^{bf}_{g,a,y,Q}\, e^{-(M/12+F^{bf}_{g,y,Q})} \\ N^{ns-s}_{g,a,y,Q+1} &= N^{ns-s}_{g,a,y,Q}\, e^{-(M/12+F^{ns-s}_{g,y,Q})} + N^{bx}_{g,a,y,Q}\, e^{-(M/12+F^{bx}_{g,y,Q})} + N^{bf}_{g,a,y,Q}\, e^{-(M/12+F^{bf}_{g,y,Q})} \end{aligned} \qquad \text{(C.1)}$$

$$N^{bx}_{g,a,y,Q+1} = N^{bf}_{g,a,y,Q+1} = 0\,.$$

Adult birds that did not attempt to breed during year y remain in the non-breeding category for the duration of the year, and suffer natural M and fishing mortality ($F^{ns-f}_{g,y,m}$ or $F^{ns-s}_{g,y,m}$) during each month (the number of non-breeding birds at the start of month *m=Q+1* is given by equation C.1), relative to their success or failure breeding the prior year

$$\begin{aligned} N^{ns-f}_{g,a,y,m} &= N^{ns-f}_{g,a,y,m-1}\, e^{-(M/12+F^{ns-f}_{g,y,m-1})} \qquad m=2\ldots(Q-1),(Q+1)\ldots 12 \\ N^{ns-s}_{g,a,y,m} &= N^{ns-s}_{g,a,y,m-1}\, e^{-(M/12+F^{ns-s}_{g,y,m-1})} \qquad m=2\ldots(Q-1),(Q+1)\ldots 12 \end{aligned}\ .$$

Similarly, juvenile and immature birds remain in their respective catagories throughout the month and suffer both natural and fishing mortality.

Juveniles and immatures share their own, sex age and density-dependent natural mortality rate $M^{J,I}_{a,y}$ (see section C.3) but have slightly different fishing mortality rates as they have different at-sea distributions (see section B.1).

$$\begin{aligned} N^{J}_{g,a,y,m} &= N^{J}_{g,a,y,m-1}\, e^{-(M^{J,I}_{a,y}/12+F^{J}_{g,y,m-1})} \qquad m = 2\ldots12. \\ N^{I}_{g,a,y,m} &= N^{I}_{g,a,y,m-1}\, e^{-(M^{J,I}_{a,y}/12+F^{I}_{g,y,m-1})} \qquad m = 2\ldots12. \end{aligned} \tag{C.2}$$

Any chicks that survive to fledge at the end of the breeding season, are added to the juvenile category, age 0, at the beginning of month Q+1. For clarity of presentation, this is not shown in equation C.2.

All eggs are assumed to be laid on the first day of the breeding season. The number of chicks (including eggs) present in the colony during the breeding season at the start of month m is given by those that survive from the previous month. Death occurs due to natural causes (e.g. environmental, or physiological) M^{0}_{y} or through the natural M or fishing related $F^{bx}_{g,y,m}$ death of either parent,

$$N^{0}_{g,y,m} = N^{0}_{g,y,m-1}\, e^{-M^{0}_{y}/12-\sum_{g'=1}^{2}\left(M/12+F^{bx}_{g',y,m-1}\right)} \qquad m = 2\ldots Q.$$

At the end of the breeding season all chicks move into the juvenile category and become vulnerable to incidental catch by fisheries (equation C.2).

C.2 Between year dynamics

At the end of each year (i.e. start of the next year), all birds move to the next age class, a proportion of each immature age class recruits into the breeding adult category (Table B.4), and some adult birds move from the non-breeding to the breeding category.

The number of breeding birds of sex *g* and age $a+1$ at the start of year $y+1$ (month 1)

$N^{bx}_{g,a+1,y+1,1}$ is given by the sum of the number of returning failed breeders (at rate ϕ_y), the returning non-breeders (also at rate ϕ_y), and the maturing juveniles (at age-specific rate λ_a),

$$N^{bx}_{g,a+1,y+1,1} = \varphi_y \left(N^{bf}_{g,a,y,13} + N^{ns-f}_{g,a,y,13} + N^{ns-s}_{g,a,y,13} \right) + \lambda_a \, N^{J}_{g,a,y,13} \qquad a = 1...A-2$$

where *A* is the maximum age and is a (a plus group) so that,

$$N^{bx}_{g,A,y+1,1} = N^{bx}_{g,A,y,13} + N^{bx}_{g,A-1,y,13} + \varphi_y \left(N^{bf}_{g,A-1,y,13} + N^{ns-f}_{g,A-1,y,13} + N^{ns-s}_{g,A-1,y,13} \right) + \lambda_{A-1} \, N^{J}_{g,A-1,y,13}.$$

Note that '13' indicates the number of birds present at the very end of month 12 of year y (i.e. the start of 'month 13') and is used for clarity of presentation so that mortality tht occurred during the last month of the year need not be shown.

No birds are assigned to the failed breeder category at the start of the year,

$$N^{bf}_{g,a+1,y+1,1} = 0 \qquad g = 1,2; \, a = 2...A-1.$$

Some adult birds take a year's sabbatical (at rate $1-\phi_y$),

$$N^{ns-f}_{g,a+1,y+1,1} = \left(1-\varphi_y\right) N^{ns-f}_{g,a,y,13} \qquad g = 1,2; \, a = 2...A-1.$$
$$N^{ns-s}_{g,a+1,y+1,1} = \left(1-\varphi_y\right) N^{ns-s}_{g,a,y,13} \qquad g = 1,2; \, a = 2...A-1.$$

Juvenile birds leave to join the adult breeding category at age-specific rate λ_a (note that surviving chicks from the previous year *y* became juveniles of age zero $N^{J}_{0,y,Q+1}$ during that year, at the end of the breeding season),

$$N^{J}_{g,a+1,y+1,1} = \left(1-\lambda_a\right) N^{J}_{g,a,y,13} \qquad a = 0...A-1.$$

The number of breeding pairs $B_{y,m}$ present in the colony during the first month of the breeding season is given by the smaller of the number of breeding males and breeding females. As

albatross only lay a single egg per breeding attemt, the number of breeding pairs is also the number of chicks (or eggs) $N^{0}_{y,1}$ at the start of the breeding season (m=1). Assuming a 1:1 sex ratio at birth

$$N^{0}_{g,y,1} = 0.5\,B_{y,1} = \min\left(\sum_{a=1}^{A} N^{bx}_{1,a,y,1},\ \sum_{a=1}^{A} N^{bx}_{2,a,y,1} \right). \qquad \text{(C.3)}$$

C.3 Density-dependence on juvenile and immature mortality

Density-dependence for juveniles and immmatures is modelled by, initially, making two key assumptions; first that the lowest mortality rate for juveniles and immatures (achieved at population size zero) is equal to that of adults M; and second, that juvenile mortality increases linearly with increasing population size, to its maximum rate M^{J}_{0} when the population is at its unfished equilibrium size N^{1+}_{0}. The $1+$ population size is given by the total number of birds aged $a = 1$ or more, in all categories c in the population at the start of year y (month $m = 1$), N^{1+}_{y},

$$N^{1+}_{y} = \sum_{c} \sum_{g=1}^{2} \sum_{a=1}^{A} N^{c}_{g,a,y,1}.$$

By simple linear regression (linear, that is, if γ=1), for any population size N^{1+}_{y} the corresponding density-dependent juvenile and immature mortality rate $M^{J,I}_{y}$ is,

$$M^{J,I}_{y} = M + \left(M - M^{J,I}_{0}\right)\left(\frac{N^{1+}_{y}}{N^{1+}_{0}}\right)^{\gamma}.$$

Juvenile and immature birds assume natural mortality rate $M_y^{J,I}$ to the age of 5, thereafter taking the adult natural mortality rate M. The shape of this function is governed by the parameter γ, which is estimated.

C.4 Density-dependence on chick mortality

Density-dependence is modelled for the chick mortality term as a function of the number of breeding pairs in the population B_y. Chick mortality (before accounting for environmental effects $\overline{M}_y^0$) is assumed to be at its lowest rate at zero population size, when it is assumed to be equal to that of adults *M*. At maximum population size chick mortality is M_0^o

$$\overline{M}_y^0 = M \exp\left[\left(B_y / B_0\right)^{\kappa} \ln\left(M_0^0 / M\right)\right] \qquad \text{(C.4)}$$

where

$$M_0^0 = -2\, M\, p^B - \ln\left(\tilde{S}_0\right) \qquad \text{(C.5)}.$$

The highest rate of chick mortality M_0^o reflects the mortality of both parents during the portion of the year represented by the breeding season p^B, and the number of chicks fledged when the population is at unexploited equilibrium $\tilde{S}_0$, which is an estimated model parameter. Given a 6 month breeding season (1 Oct to end March) p^B=1/2. The parameter κ controls the level of density-dependent compensation (κ=0 gives density independent chick mortality) and is also an estimated parameter.

Environmental variables further influence the realized chick mortality rate in year *y* M_y^0, see section C.5.

C.5 Environmental variables

Environmental variables cause the chick mortality rate M_y^0 in a given year *y* to deviate from the average level $\overline{M}_y^0$ given by equation C.4)

$$M_y^0 = \overline{M}_y^0 \sum_{i \in I} f(x_i)$$

Where $f(x_i)$ is a functional relationship for environmental covariate x_i (of the set of covariates *I* used by the model). A flexible, exponential, functional form was used

$$f(x_i) = \exp\left(\theta_i \; x_i^{\,b}\right).$$

Here the parameters θ_i , termed "slope" parameters are estimated by the model whereas the *b* parameter is fixed at 1.

C.6 Modeling incidental catch

The instantaneous fishing mortality rate $F_{g,y,m}^c$ for birds in any category c of sex *g* during month m of year y is calculated from the number of birds caught during the month $C_{g,y,m}^c$ by assuming that all birds are caught in a pulse at the middle of each month, after half the month's natural mortality has occurred,

$$F_{g,y,m}^c = -log\left(1 - \frac{C_{g,y,m}^c}{\sum_{a=1}^{A} N_{g,y,m}^c \; e^{-0.6M/12}}\right)$$

Note that fishing mortality rates depend on the at-sea distribution of each catagory (Table B.1). The relative susceptibility of different classes of black-browed albatross to bycatch has not been

explored in this study and is assumed to be proportional to the overlap with a given fleet / super-fleet.

To model the total catch $C^{c}_{g,y,m}$ of birds from category c of sex g taken during month m of year y, the catch of birds of each age a in each 5° x 5° cell b by each fishery f is summed. The catch in a particular cell b is a function of the number of birds in the population at the middle of the month $\overline{N}^{c}_{g,a,y,m}$, present in cell b at that time. Presence in cell b is given by $P^{c}_{y,m,b}$ the proportion of the birds from category c that have been observed to occupy cell b (i.e. the at-sea distribution), multiplied by $P^{S}_{g,m}$ the number of birds that are likely to be at sea. This is, in turn, multiplied by the effective number of hooks (longline) deployed or hours (trawled) fished in that cell at that time, which is given by the product of the total recorded number of hooks $E^{f}_{y,m,b}$ deployed by each fishery f multiplied by the model estimated 'catchability' of hooks for fishery f, q^{f}, inflated by the greater catchability of the proportion of the population that belongs to the more susceptible type. The total effective number of hooks is calculated by summing across all fisheries f. The total catch during month m of year y is given by summing over all sexes g, ages a and 5° x 5° cells b,

$$C^{c}_{y,m} = \sum_{g,a,b}\left(\overline{N}^{c}_{g,a,y,m} \; P^{c}_{y,m,b} \; P^{S}_{g,m} \sum_{f} q^{f} \left(1 + p^{B}_{y,m} \; q^{B}\right) E^{f}_{y,m,b} \right). \qquad \text{(C.6)}$$

The number of birds in the middle of the month $\overline{N}^{c}_{g,a,y,m}$ is given by the product of the numbers at the start of the month $N^{c}_{g,a,y,m}$ and half the natural mortality for birds of age a in category c.

C.7 Matching observed bycatch rate

For each of the observed bycatch rates by super-fleet collected from the literature, the model estimates a bycatch rate for the study area (matched as closely as possible by one or more 5˚×5˚ cell) over the years and months during which the data were collected (Table B.3). To apportion bycatch to the focal population on Kerguelen, it is important to note that BBA from other colonies can make up a significant proportion of the observed BBA bycatch. To estimate the probability that a given BBA bycatch observation involved an individual from the focal population we calculated a 'population multiplier'. This value is calculated from the proportion of BBA from the focal colony versus other colonies and is used to scale the reported bycatch rate to a focal-colony specific bycatch rate estimate. This involved first estimating the number of individuals from a given colony in each bycatch area (a) as follows:

$$N_a = P_a pop.size$$

where a is a study from which a bycatch rate was reported and relates to a given spatial area and time period, P_a is the observed proportion of individuals of a given colony in a given area of reported bycatch and $pop.size$ is the population size estimated by multiplying the global population by the % of the global population a given colony represents (ACAP, 2012) The probability that a BBA caught in a given bycatch area originated from the focal population was then estimated as

$$p_i^G = \frac{N_G}{\sum_Z N_Z}$$

where N_z is the number of individuals from a BBA colony other than Kerguelen, N_G is the number of BBA from Kerguelen.

The proportion of individuals from other populations was estimated in different ways, depending upon access to data and distribution at-sea maps. We focused on BBA populations in

Seabird Tracking Database (www.seabirdtracking.org)) that overlapped the distribution of our focal colony (Bird Island, South Georgia and Islas Diego Ramírez), as well as Macquarie (Terauds et al., 2006), as they also overlap. The proportion of Bird Island originating BBA was calculated from individual tracks shared through Seabird Tracking Database (BirdLife International, 2004; R. Phillips, datasets; 457, 492, 493). Locations of BBA from Diego Ramirez were estimated visually using Seabird Database as the proportion of locations that appeared in a bycatch area. Lastly, the proportion of BBA from

Macquarie in each bycatch area was approximated by distribution at-sea maps (Terauds et al., 2006). The temporal and spatial location of bycatch is described in Section B.4, Table B.3. If a reported BBA bycatch occurred during breeding and non-breeding periods, the total number of birds occurring in the area across seasons was used.

C.8 Initial conditions

We assume the population is at an unfished equilibrium at the beginning of the modeling period (1950). We calculate the juvenile and immature natural mortality rate ($\overline{M}_0^{J,I}$) that will maintain the population at this unfished equilibrium, given the resource dynamics equations shown above, the assumed adult natural mortality rate M and the pristine chick natural mortality rate M^0 (from equation C.5 and model parameter $\widetilde{S}$).

Initial values for estimated parameters were based on observed demographic data (population size; 1,310) productivity (0.673; Barbraud et al., 2011)), juvenile / immature mortality (0.72; Nevoux et al., 2010b, does not consider density-dependence).

C.9 Fitting procedure

The demographic response variables (i.e. for which data time series exist) are the numbers of breeding pairs at the start of each year $B_{y,1}$, the numbers of chicks fledged at the end of the breeding season $N^{J}_{0,Q+1}$, the annual adult survival rate S^{A}_{y}, and juvenile survival to age 5 S^{J}_{y}. The number of breeding pairs in the population at the time of census $B_{y,1}$ is given by equation C.3. The number of chicks fledged $\tilde{S}_{y}$ in year *y* is given by the number of chicks fledged at the end of the breeding season $N^{J}_{0,Q+1}$ (they are allocated to the juvenile category at the start of the first month after the breeding season ends, *Q*+1) divided by the number of pairs that made a breeding attempt,

$$\tilde{S}_{y} = N^{J}_{0,Q+1} \big/ B_{y,1}$$

Adult survival S^{A}_{y} (a percentage) is given by,

$$S^{A}_{y} = 100\, N^{A}_{y+1} / N^{A}_{y}$$

where

$$N^{A}_{y} = \sum_{a=1}^{A} \sum_{c \in (bx,bf,ns)} N^{c}_{a,y,1}\,.$$

and *A* is the maximum age group in the model (a plus group).

The juvenile and immature survival rate to age 5 (a percentage) is,

$$S^{J,I}_{y} = 100\, e^{-Z^{J,I}_{y}},$$

where $Z^{J,I}_{y}$ is the total mortality rate over the previous 4 years for immatures that are aged 5 at the start of year y,

$$Z^{I,J}_{y} = \sum_{y'=y-3}^{y} \left[\sum_{a=1}^{4} M^{J,I}_{a,y'} + \sum_{m=1}^{12} F^{I,J}_{y',m} \right].$$

Juvenile and immature survival to age 5 $S_y^{J,I}$ cannot easily be expressed in terms of a ratio of the numbers of juveniles present in various years because birds leave the juvenile category through maturation, not just through mortality.

Note that the annual breeding success is given by the number of chicks fledged divided by the number of breeding pairs. Therefore one can choose to condition the model on any two of the three quantities: number of breeding pairs, number of chicks fledged, or breeding success. Finally, a response variable was calculated to match the observed bycatch rate, representing numbers of birds per thousand trawl hours, observed in a specified set of 5˚ cells over a span of months by the trawl super-fleet. This was given by the estimated catch in number of birds C_i divided by the effort in thousands of trawl hours E_i over that region and time, for the single bycatch observation *i*,

$$R_i = C_i/E_i .$$

The number of birds caught C_i is estimated in the same way as $C_{y,m}^c$ in equation C.6, with appropriate summation over 5° x 5°cells and time periods and over all categories c.

C.10 Likelihood

Maximum likelihood was used to estimate the model parameters. Normal distributions are assumed for the residuals for the expected $\boldsymbol{B}_{y,1}$ and observed $B_{y,1}^{obs}$ number of breeding pairs,

$$\boldsymbol{B}_{y,1} \sim N\left(B_{y,1}^{obs}, \sigma_B\right)$$

for all years *y* for which observations exist. Similarly, a normal distribution is assumed for the residuals of the expected $\tilde{S}_y$ and observed $\tilde{S}_y^{obs}$ numbers fledged for all years *y* for which observations exist,

$$\tilde{S}_y \sim N\left(\tilde{S}_y^{obs}, \sigma_{\tilde{S}}\right).$$

Values of σ_B = 150.4241 and $\sigma_{\tilde{S}}$ = 155.3963 were obtained using iterative re-weighting.

A binomial distribution was assumed for the adult survival rate, along with an assumed effective sample size of 100 animals, which seemed to achieve a good balance with the other data sources. The binomial probability was given by the observed survival rates $p = S_{y,1}^{A,obs}$, and the number of observations was the integer part of ($100\,S_y^A$) out of 100 trials.

$$100\,S_y^A \sim Binom\left(100,\ S_{y,1}^{A,obs}\right)$$

Similarly, for juvenile and immature survival,

$$100\,S_y^{J,I} \sim Binom\left(100,\ S_{y,1}^{J,I,obs}\right)$$

Given the broad range of data sources and values for the estimated bycatch estimates within and across fleets (Table B.3), bycatch for all super-fleets was placed at 2.2659e^3; the greatest observed varaibility in bycatches across super-fleets. Although somewhat arbitrary, this allowed bycatch observations to be equally weighted across fleets.

C.11 Estimated parameters

The estimated parameters of the model are the number of chicks fledged at unexploited equilibrium $\tilde{S}_0$, the number of breeding pairs *B*, the adult natural mortality rate *M*, the parameters governing density-dependence for juvenile and immature birdsγ, and for chicksκ; the

catchability parameters for the Japanese mitigated pelagic longline south of 30° S q^j, other pelagic longline q^p, demersal longlinline q^d trawl q^t, and illegal demersal longline q^{iuu} super-fleets; and the three environmental parameters θ_i.

Appendix D: Sensitivity of model estimated parameter values to the estimated IUU demersal longline data

The sensitivity of the model to the estimated IUU data was assessed by comparing the parameter estimates from a null model (with no environmental variables) assuming

(i) the estimated IUU effort and bycatch rate and the same bycatch rate for the Japanese as other pelagic longline fleets

to alternative models with the following assumptions;

(ii) no IUU effort,

(iii) no IUU effort, and Japanese bycatch rate allowed to differ from other pelagic longline fleets,

(iv) twice the estimated magnitude of IUU effort,

(v) half the estimated magnitude of IUU effort,

(vi) no fitting to the observed IUU bycatch rate, and

(vii) the largest estimated bycatch population multiplier in the model (4.33×10^{-3}), is applied to the IUU observation instead of the original value (8.71×10^{-4}). See Appendix B.7 for details on the calculation of these population multipliers.

We also assess the impact of the estimated magnitude of IUU effort on the:

(viii) 'Ix' model, which allows the sea-surface temperature (SST) near Kerguelen during the incubation period to influence chick mortality,

with a model that differed from the Ix model in that it had:

(ix) no IUU effort.

Table D.1 *Final parameter estimates for the models (i – ix) assessing the sensitivity of the albatross population model to estimated IUU demersal longline fleet data. Model names correspond to i - ix and are briefly described for ease of interpretation. 'Japan sep.' = Japanese mitigated pelagic longline fleet south of 30S bycatch rate can be estimated. 'negLnL' = negative loglikelihood, 'popmulti' = population multiplier. alpha = juvenile and immature mortality rate including density-dependence (which is the same value), NBop = number of breeding pairs, qJpel = Japanese mitigated pelagic longline super-fleet bycatch south of 30˚ S rate, qpel = other pelagic longline super-fleet bycatch catchability, qdem = demersal longline super-fleet bycatch catchability, qill = illegal, unreported and unregulated super-fleet bycatch catchability, qtrawl = trawl super-fleet bycatch catchability, MCpar= chick mortality rate including density-dependence, prod = productivity of the albatross population, inc = slope of the relationship between the average SST near Kerguelen during the incubation period and chick mortality. 'Fledge' = chicks fledged, 'Sjuv' = juvenile survival, 'Sadult' = adult survival, 'Sum' = sum of likelihood components excluding 'Bycatch'. '*[a]*' indicates that the catchability was not estimated separately from other pelagic longline fleets. Madult = adult mortality. See Appendix B).* *[db]* *' indicates models whose negative log likelihood values cannot be compared with those of any other model presented here due to differences in the data used. All log likelihood values without a superscript can be compared with one another.*

parameter	model								
	(i) null	**(ii) no IUU effort, Japan sep.**	**(iii) no IUU effort**	**(iv) 2x IUU effort**	**(v) half IUU effort**	**(vi) IUU, no observed bycatch**	**(vii) IUU, larger popmulti**	**(viii) Ix**	**(ix) Ix, no IUU**
negLnL	299.03	302.28[b]	304.23[b]	299.03	299.03	299.03[b]	299.06[c]	294.69	302.91[b]
alpha	8.62	6.97	5.79	8.62	8.62	8.62	8.62	10.69	17.12
NBop	1118	1087	1054	1118	1118	1118	1118	1115	1050
qJpel[a]	3.58E-10	8.08E-10	3.58E-10	3.58E-10	3.58E-10	3.58E-10	3.58E-10	3.58E-10	3.58E-10
qpel	3.58E-10	7.15E-10	3.58E-10	3.58E-10	3.58E-10	3.58E-10	3.58E-10	3.58E-10	3.58E-10
qdem	1.48E-09	1.30E-8	2.37E-09	1.48E-09	1.48E-09	1.48E-09	1.48E-09	2.10E-09	2.37E-09
qill	1.62E-08	-	-	8.10E-09	3.24E-08	1.62E-08	1.62E-08	1.59E-08	-
qtrawl	8.43E-08	1.02E-07	1.15E-07	8.43E-08	8.43E-08	8.43E-08	8.43	8.46E-08	1.19E-07
MCpar	0.731	0.729	1.02	0.731	0.731	0.731	0.722	0.616	1.07
prod	0.565	0.554	0.569	0.565	0.565	0.565	0.558	0.569	0.563
inc	-	-	-	-	-	-	-	-0.511	-0.099
Components of the likelihood -		-	-	-	-	-	-	-	-
Nbp	166.9	166.24	167.31	166.9	166.9	166.9	166.93	166.91	167.39
Fledge	167.33	168.32	168.55	167.33	167.33	167.33	167.65	164.06	168.28
Sjuv	54.38	55.57	57.29	54.38	54.38	54.38	54.06	53.3	56.11
Sadult	23.47	23.88	24	23.47	23.47	23.47	23.47	23.45	24
Sum	412.08	414.01	417.15	412.08	412.08	412.08	412.11	407.72	415.78
Bycatch	-113.05	-111.73	-112.91	-113.05	-113.05	-113.05	-113.05	-113.03	-112.87

There was relatively little change in the estimated parameter values across models (Table D.1). Note that models iv and v do not alter the model at all, they merely change the "unit" of effort for the bycatch fleet, thereby alter the unit of the estimated catchability parameter. Halving the effort simply doubles the catchability estimate and vice versa for doubling it. As expected, the parameters estimated in models i, iv, v, and vi produce virtually identical modelled, as evidenced by the partial likelihoods. This clearly demonstrates that the allocation of the majority of bycatch to the IUU fleet was not due to the assumed magnitude of effort. Similarly, altering the bycatch assumptions regarding the observed bycatch value by not fitting to this value (model vi), or increasing it (model vii; through increasing the population multiplier) had little effect on estimated parameter values, including the catchability for the IUU fleet. Models that exclude the IUU super-fleet (models ii, iii, and ix) attributed the IUU bycatch to the legal demersal or trawl super-fleets, or both. However, these models also show overall poorer agreement with the observations, compared with the models that include the IUU super-fleet (see individual likelihood components, Table D.1).

5 Cumulative impacts of climate change and fleet dynamics on a southern Indian Ocean albatross colony

5.1 Abstract

Determining if albatross populations will be self-sustaining given future climate change requires an understanding of the factors impacting population growth and how those factors are likely to change. Research indicates that albatrosses are impacted by environmental as well as fisheries factors. While projections of environmental variables given climate change are widely available, the behavior of fleets and consequent distribution and magnitude of fishing effort is seldom explicitly considered. Here we broaden the understanding of climate change impacts on albatrosses by incorporating fleet behavior into population dynamics models. This is achieved by combining the projected distribution of Japanese and Taiwanese pelagic longline effort from fleet dynamics models into an integrated population model for black-browed albatross (BBA) breeding on Kerguelen Islands. Additionally, the impacts of climate change on breeding success are also projected. We create four projections, assessing all combinations of the following assumptions: past (historical) or future (predicted) distribution of fishing effort and past or future sea-surface temperature. We then evaluate the relative impact of the projected effort and change in SST on BBA given each combination of assumptions. Results indicate that the future impacts of pelagic longline bycatch on the bycatch of Kerguelen BBA, including Japanese and Taiwanese fleets, will be minimal, with virtually no bycatch estimated for pelagic longline fleets for either effort distribution assumption. Estimated annual bycatch for demersal longline and trawl fleets was very low, totaling around nine birds per year, cumulatively. This was true for both SST assumptions. Interestingly, the projected increase in SST is likely to result in a lower

number of breeding pairs (~1,030) relative to a continuation of the current SST (~1,100). Specifically, increasing SST during the breeding period reduces chick mortality, resulting in high numbers of fledged chicks. However, the density-dependent sensitivity of juveniles to the total number of birds in the population results in an increase in juvenile mortality, ultimately reducing the number of breeding pairs. Models incorporating the impact of climate change on fleet dynamics and interacting populations provide novel insight into complex systems and the capacity to enhance manager's ability to mitigate the impacts of climate change and fisheries interactions.

5.2 Introduction

The Southern Ocean is one of the most rapidly changing pelagic environments (Gillett and Thompson, 2003; Levitus et al., 2005) with these changes expected to continue into the future (IPCC, 2013). Shifts in seabird phenology (Chambers et al., 2013) and distribution (Johnson et al., 2011; Weimerskirch et al., 2012) have already been observed. However, the response of individual species will vary by region (Constable et al., 2014) and will continue to alter foodwebs and ocean ecosystems (Hoegh-Guldberg and Bruno, 2010; O'Connor et al., 2009; Trathan et al., 2007). This complicates the management of interacting species and the ecosystems they rely on.

Human influences are important to include when considering the future of our oceans. Mounting evidence indicates that humans have, directly or indirectly, affected species (Hoegh-Guldberg and Bruno, 2010; Nagelkerken and Connell, 2015), in many regions (van Sebille, 2015) and depths of the ocean (Levitus et al., 2005). Industrial fishing in the form of pelagic longline effort targeting tunas has occurred in the Southern Ocean since the 1950s (Moreno and

Herrera, 2013; Tuck et al., 2003). Unfortunately, incidental capture (bycatch) of non-target species, particularly albatross, is thought responsible for many population declines (Baker et al., 2002; Brothers, 1991; Klaer and Polacheck, 1997; Tuck et al., 2001).

While a reduction in bycatch has resulted in some populations rebounding (Robertson et al., 2014), the synergistic impacts of future environmental change and fisheries bycatch are likely to shape the viability of albatross populations (Rivalan et al., 2010; Thomson et al., 2015). Differentiating the relative and quantitative impact of multiple covariates on a popoulation can be achieved using an integrated model framework (Thomson et al., 2015; Tuck et al., 2015). By incorporating all datasources (environmental, fisheries, demographics) into the estimation framework, this approach enables separation of observed mortality rates and the theoretical mortality rates for a population unimpacted by other covariates (e.g. bycatch), fleet-specific bycatch rates and the impacts of density-dependence on chick, immature and juvenile albatross mortality. Furthermore, this approach specifies the relative independence of the estimated parameter values from one-another, which reflects confidence in the parameter estimates.

Applied to a black-browed albatross population breeding on Kerguelen (Ch. 4), this approach indicates that illegal, unreported, and unregulated (IUU) demersal longline effort appears to have been responsible for the majority of historic bycatch, with lower numbers of birds caught in legal pelagic and demersal longline and trawl effort. Additionally, warm sea-surface temperature (SST) during the incubation period relates to higher chick surival, supporting the apparent recovery of this population.

The majority of research projecting envioronmental and fisheries bycatch impacts on albatross population demographics given climate change relies exclusively on historic distributions of fishing effort, with alterations to the magnitude (Rolland et al., 2009b) or bycatch

rate (Rivalan et al., 2010; Thomson et al., 2015). Given predicted shifts in many tuna species (Dueri et al., 2014; Lehodey et al., 2015; Lehodey et al., 2010) and associated catch (Dell et al., 2015), effort is unlikely to remain static. However, the response of fishers to changes in species distributions may not match the new distributions due to other social and / or economic factors (Pinsky and Fogarty, 2012).

Despite the complexities of predicting fisher behavior (Dowling et al., 2013; Mangel et al., 2015), the potential for unintended consequences to management actions demonstrates the value of increasing this capacity (Abbott and Haynie, 2012; Chan et al., 2014; Fulton et al., 2011). This has led to studies using dynamic-state-variable-models to evaluate the fisher decision-making process (Dowling et al., 2013; Dowling et al., 2012) and the efficacy of economic incentives on reducing bycatch, including seabirds (Mangel et al., 2015; Pascoe et al., 2013).

However, this approach requires highly detailed information on the economics of vessels (Dowling et al., 2012) or high-resolution (shot by shot) effort data (Mangel et al., 2015; Pascoe et al., 2013). As these types of data are unavailable for many of the fleets in the Southern Ocean, an alternative approach to modeling pelagic longline effort in the southern Indian Ocean has been developed and used to predict the impact of climate change on the distribution of fishing effort (Ch. 3). Specifically, the observed distribution of effort was compared to the distribution of effort modelled by a range of fishing strategies, each combining different aspects of the fishery. After incorporating climate change predictions in the associated aspects of the fishery, the strategy most similar to the observed effort (hereafter: historic effort allocation strategy) was then used to project the distribution of effort given climate change. The results indicated slight

shifts in the average distribution of effort relating to the historic effort allocation strategy and the relative targeting of different tuna species.

This type of model and projection can provide dynamic insight into the currently static view of fisheries impacts on albatross demographics. Of the fleets assessed in the model of BBA population dynamics, the IUU fleet associated with bycatch in the model has been virtually inactive since the late 2000's and is assumed to be absent in the future. Both demersal longline and trawl fleets are spatially constricted to shelf habitats in terms of their potential response to climate change (assuming the same target species are maintained). Therefore, the Japanese and Taiwanese pelagic longline fleets provide an interesting opportunity to assess the impacts of including or excluding projected shifts in the distribution of effort when modeling albatross population dynamics.

In this study we synthesize two existing model frameworks to project the combined impacts of climate change on fleet dynamics and albatross population dynamics using the BBA colony on Kerguelen as a study case. Using projected SST from climate simulations using the BLUElink model (Oke et al., 2008), we apply the integrated population model (Ch. 4), and incorporate the predicted distribution of effort for the Japanese and Taiwanese pelagic longline fleets developed in Michael et al. (Ch. 3). Allowing a shift in the distribution of effort based on fleet dynamics enhances the value and inference gained from an integrated modeling framework. This integrated approach to assessing the potential impacts of climate change and fisheries bycatch on albatrosses provides novel information and insight to managers and users of this complicated oceanic system.

5.3 Methods

This study combines two existing modeling studies: 1) an integrated population model characterizing environmental and fisheries impacts on the BBA colony on Kerguelen Islands (Ch. 4; *albatross population model*) and 2) a fleet dynamics model projecting the impacts of climate change on Japanese and Taiwanese pelagic longline effort (Ch. 3; *fleet dynamics model*s). The impacts of climate change on BBA demographics are then projected by updating two components of the albatross population model; environmental covariates identified in Ch. 4 as impacting fledging success and the distribution of Japanese and Taiwanese fishing effort, as indicated by the fleet dynamics model.

5.3.1 Albatross population model

We use the parameter estimates from an integrated population model (Ch.4) to project the impacts of climate change on BBA breeding on Kerguelen. This integrated framework incorporates all sources of data: environmental, demographic and fisheries into the estimation framework. This approach has successfully been applied to other populations (Thomson et al., 2015; Tuck et al., 2015) and used to project future population trajectories (Thomson et al., 2015). This model operates at a monthly, $5^{\circ} \times 5^{\circ}$ temporal and spatial scale and is structured by sex, age-class, breeding stage, and reproductive history of individual albatrosses. It quantifies the bycatch of each of 5 super-fleets (fleets grouped by gear-type and reported bycatch rates): Japanese pelagic longline, non-Japanese pelagic longline (including the Taiwanese fleet), demersal longline, trawl and illegal, unreported and unregulated (IUU) demersal longline. For this population, the estimated bycatch was greatest for the IUU fleet but occurred in all super-fleets in Ch. 4. It was also found that relatively average SST near the colony during incubation relates to increased chick survival. Although the Japanese and Taiwanese fleets are not a major

source of bycatch for this population, changes in overlap between birds and effort can alter the frequency of bycatch. As even small changes in adult mortality can have significant impacts on albatross populations, the future distributions of these fleets could impact population dynamics.

5.3.2 Fleet dynamics models

We use the projected distribution of Japanese and Taiwanese pelagic longline effort in the southern Indian Ocean as described in Ch. 3. These models assume fleets allocate effort based on an effort allocation strategy minimizing the uncertainty in CPUE predictions, with different emphases on the CPUE of the four modelled target species based on fleet-specific relationships. This effort allocation strategy was identified from four strategies assessing different combinations of value, cost, and variability of CPUE, as the most related to the observed distribution of effort. Shifts in effort were projected by incorporating environmental variables into CPUE distribution models for four tuna species and obtaining the projected uncertainty in modelled CPUE. These projected distributions are incorporated into the albatross population model (see 'climate change projection' for details)

5.3.3 Climate change projection

Climate change forecast data are generated by the Ocean Eddy-resolving Model (Matear et al., 2013; Oke et al., 2008; Sun et al., 2012) within BLUElink, based on corrected output from the CSIRO Mk.3.5 output which is forced by the A1B scenario for the 2060s (Hartog et al., 2011). Data are monthly, and, as they were produced on an irregular grid, were aggregated to a 5°× 5° scale for CPUE models or calculated across the area and months of interest regarding the average SST near Kerguelen during the incubation period. We assume that the albatross incubation period (October-December) will not change in the future. Data on SST, sea-surface height anomaly (SSHa), and phytoplankton from 2063-2068 were extracted, with tuna CPUE

models requiring two of each of these variables depending on the targeted fish species (see Ch. 3 for details). To convert phytoplankton data to Chl values, we multiplied phytoplankton values by 1.59. This conversion factor assumes 50 mg Carbon to 1 mg Chl (Eppley et al., 1998; Sharp et al., 1980). The SST for the years between the last observed data within BBA model and the BLUElink data were linearly interpolated based on the average BLUElink SST, as there was no clear temporal trend in the BLUElink data.

The effort projections made in Ch. 3 were applied to the albatross population model. Due to current model constraints, the average distribution of effort for the projected years (2063-68) was used for the two modelled (Japanese and Taiwanese pelagic longline) fleets. For the remaining fleets in the albatross population model, projected effort was assumed to be the same as the last year of available effort data, which varied by fleet, from 2004 to 2011. Therefore, effort is projected (Japanese and Taiwanese pelagic longline) or assumed (remaining fleets) from 2012 through 2068. Fleets assumed to be inactive or with negligible bycatch in projected effort include: French and Ukrainian trawl in the Kerguelen EEZ, IUU demersal longline fleet, and Chilean demersal longline targeting toothfish (Appendix B.3 Table B.2).

5.3.4 Impact of including projected fleet dynamics

To assess the impact of including the projected distribution of effort on albatross demographics, we evaluated four different projections, assessing all combinations of the following assumptions: past versus future distribution of fishing effort (Ch. 3) and past versus future SST (derived from the BLUElink model). This produced the following projection: i) past effort and past SST, ii) future effort and past SST, iii) past effort and future SST, and iv) future effort and future SST.

5.4 Results

The average SST during the incubation period near Kerguelen increased significantly across the study period (Fig. 5.1, df = 37, $p < 0.001$).

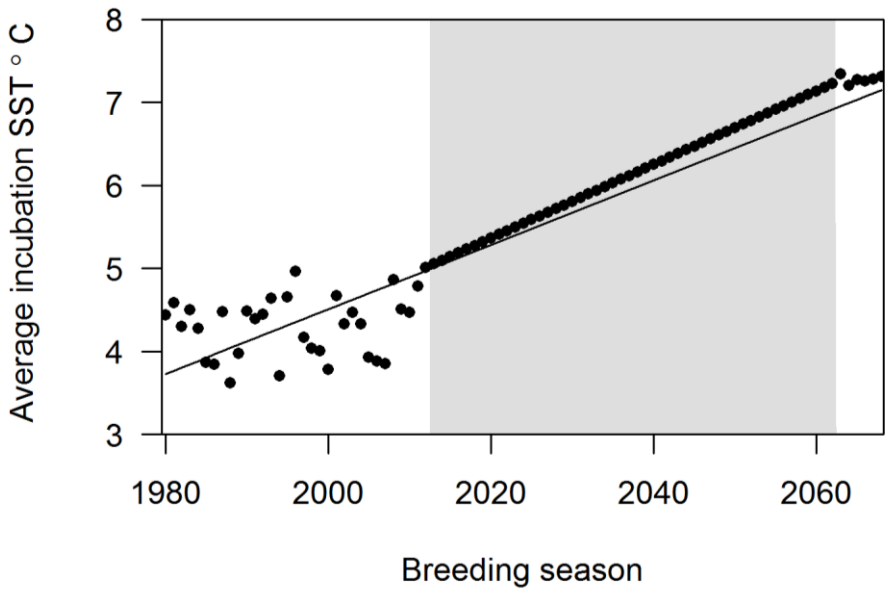

Figure 5.1*. Time series of the average SST during the incubation period near Kerguelen from 1981 to 2068. Grey shading indicates linear interpolation between observed and projected SST.*

The bycatch estimates by super-fleet were virtually identical across models (Fig. 5.2). Bycatch estimates were highest for the legal demersal longline and trawl fleets at five or four birds per year, respectively (Fig. 5.2c, d). Slight differences in bycatch estimates were less than an individual bird. Both Japanese mitigated and other pelagic longline fleets, including the Taiwanese fleet, were projected to have virtually zero bycatch (Fig. 5.2a, b). As we assumed no IUU demersal longline effort will occur in the future, 0 bycatch was estimated for this fleet (Fig. 5.2e).

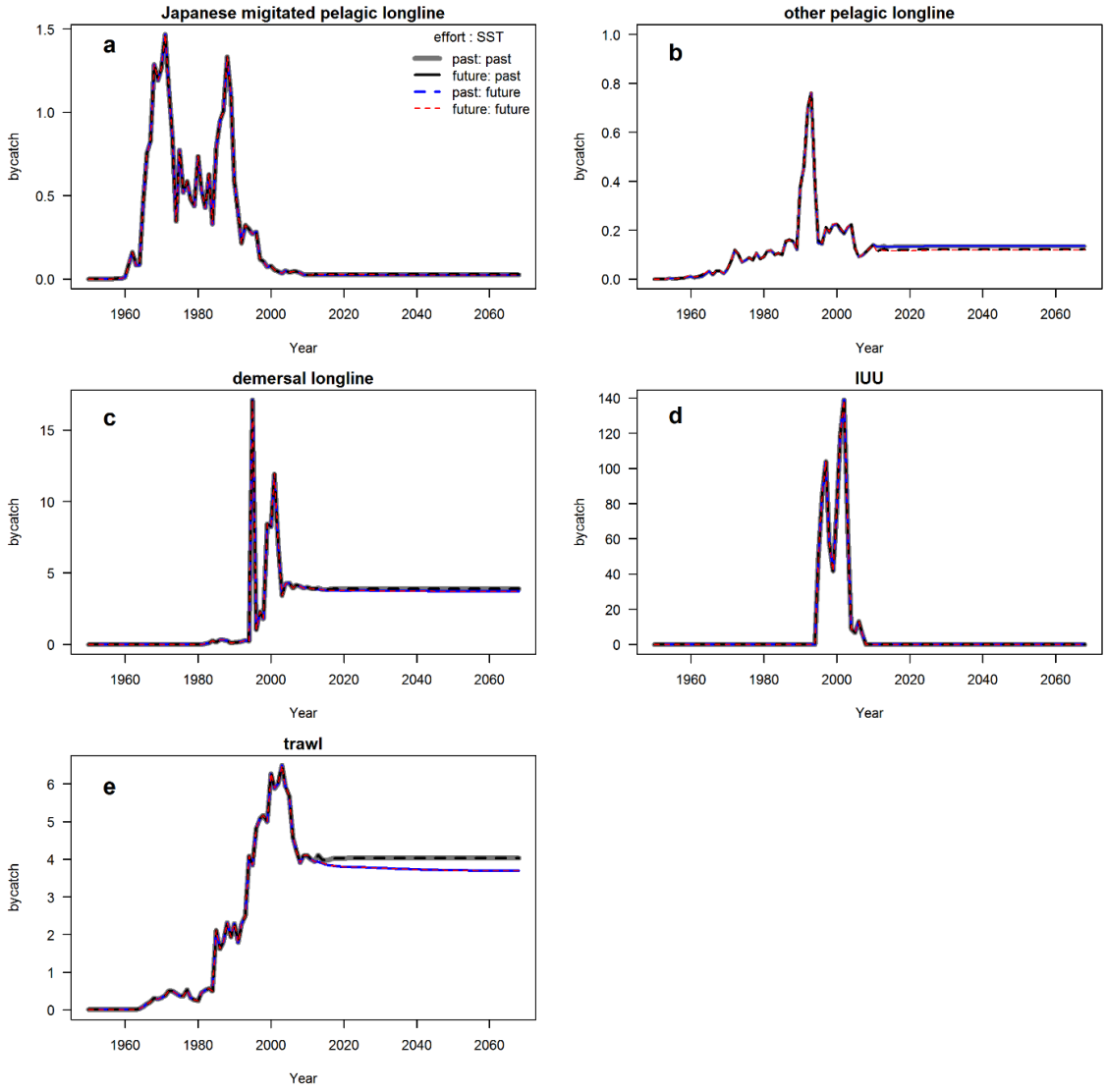

Figure 5.2 *The annual projected bycatch by super-fleet through 2068 for projections using different combinations of effort and sea-surface temperature assumptions. 'past' indicates the last year of observed effort or historical SST. 'future' indicates the projected distribution of Japanese and Taiwanese pelagic longline effort as modelled in Ch. 3 or projected SST from the BLUElink modelled data (Fig. 5.1). The projections assume the following effort: SST assumptions: (grey line) past: past, (black line), future: past, (blue dash) past: future and (red dash) future: future.*

Assuming the historically based demographic parameter estimates (Ch. 3), the impact of climate change on the Kerguelen BBA demographics was quite similar using either the past or future effort distributions (Fig. 5.3). However, the response of the population differed with the

assumed SST pattern. Specifically, assuming past SST results in all parameters essentially stabilizing near the current levels. Conversely, assuming the future SST reduces the number of breeding pairs, dramatically increases the number of chicks fledged and decreases juvenile survival relative to the projections assuming past SST.

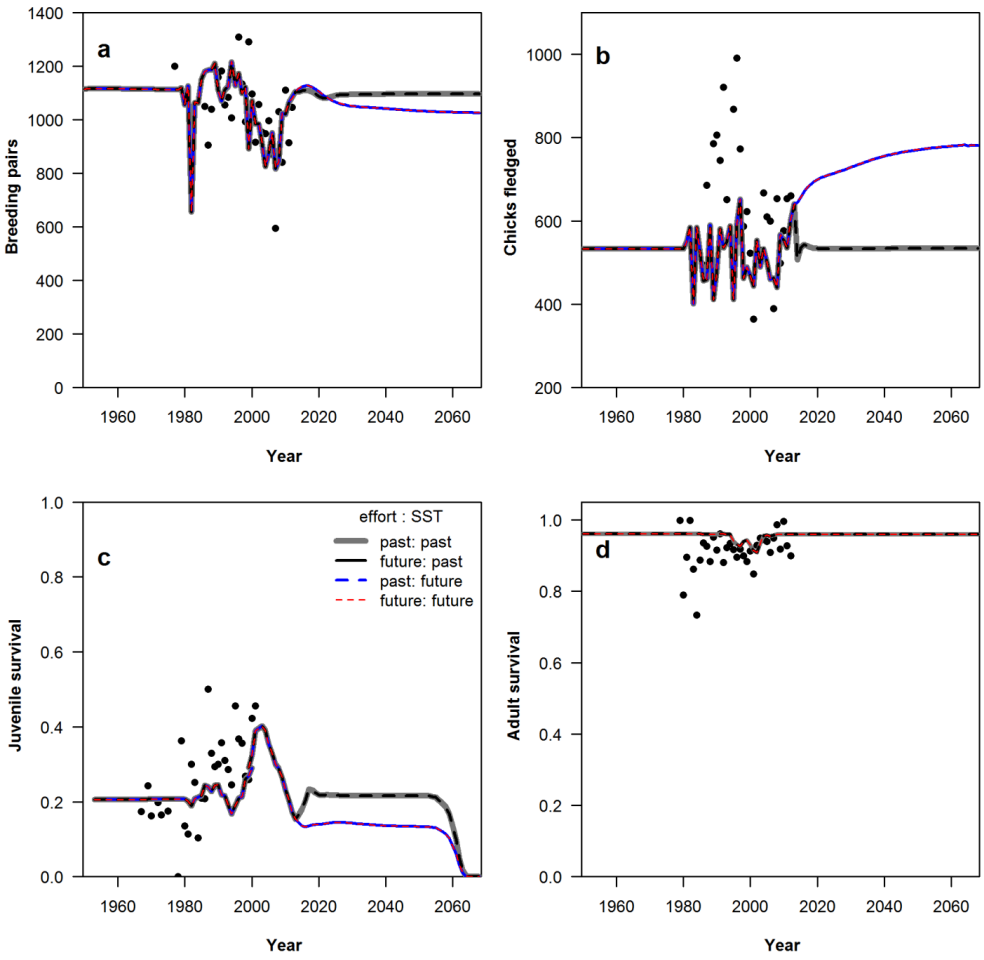

Figure 5.3 *Time series of (circles) observed and (lines and dashes) modelled (a) number of breeding pairs (b) number of chicks fledged (c) average survival to age 5, and (d), adult survival expressed as a percent, for projections using different combinations of effort and sea-surface temperature assumptions. 'past' indicates the last year of observed effort or historical SST. The projections assume the following effort: SST assumptions: (grey line) past: past, (black line), future: past, (blue dash) past: future and (red dash) future: future. 'future' indicates the projected distribution of Japanese and Taiwanese pelagic longline effort as modelled in Ch. 3 or projected SST from the BLUElink modelled data (Fig. 5.1).*

5.5 Discussion

Our findings indicate that the Kerguelen BBA population, though unlikely to be strongly impacted by bycatch in the projected future, is likely to slowly decline as a result of climate change. This population is recovering from a historical decline in the 1990's to early 2000's, which has been attributed to the now virtually absent IUU demersal longline fleet (Ch. 4). With relatively little bycatch from other fleets (Ch. 4 Fig. 4.5, Fig. 5.2), including pelagic longline fleets, and the positive impact of warming SSTs during the incubation period on breeding success, there is little inhibiting the modelled future growth of this population beyond density-dependence. Given the lack of sensitivity to the magnitude of pelagic longline effort indicated through our model comparison (Fig. 5.2), the similarity between the projected impacts of climate change in the static and projected effort distribution models (Fig. 5.3) is not surprising.

Although initially counterintuitive, the positive impact of increasing SST during the incubation period on chick fledging propagates a decline in the number of breeding pairs as a consequence of juvenile and immature density-dependence. Specifically, greater numbers of chicks fledged each year (Fig. 5.3b) with increasing SST produces more juveniles and immatures in the following years. While chick mortality is sensitive to the number of breeding pairs (Appendix C.4), juvenile and immature mortality are sensitive to the total number of birds in the population (C.3). Thus, the increased number of young birds results in an increasing mortality rate, reducing their survival to maturity (Fig. 5.3c). This density-dependent reduction in juvenile survival is severe enough to reduce the number of breeding pairs, despite virtually no change in adult mortality (Fig. 5.3d). These findings are in agreement with recent work, identifying a high sensitivity of young albatross to density-dependence related to population size (Fay et al., 2015). Thus, this study provides further support for the theory that the impacts of increasing population

density are visible within a population through decreased juvenile survival (Eberhardt, 2002). The increasing number of studies demonstrating the importance of density-dependence in long-lived seabird populations (e.g. Fay et al., 2015; Francis and Sagar, 2012; Thomson et al., 2015, Ch. 4, the current study) indicates a broader impact of density-dependence than is currently understood.

5.5.1 Colony-specific implications of projected impacts

Earlier work on this population had identified a moderately negative relationship of pelagic longline effort in the southeastern Indian ocean, particularly south of Australia (Rolland et al., 2008; Rolland et al., 2010), indicating the importance of bycatch from this fleet. Applying this relationship to the projected impacts of climate change would likely indicate a greater role of pelagic longline bycatch on the focal population. However, our application of an integrated population model including more recent demographic information (through 2011 versus 2006) did not suggest a notable impact of pelagic longline bycatch (Ch. 4). This difference likely relates to the notable increase in the number of breeding pairs since 2006 (Fig. 5.3), which would alter adult survival estimates and therefore the relative impact of bycatch on adult mortality. As our parameter estimate for the adult mortality rate assumes no impact of fisheries bycatch and a unique bycatch parameter is estimated for each fleet, a direct comparison of estimated adult mortality rates is not appropriate.

Similarly, the negative relationship of warming SSTs in the wintering ground with breeding success (Rolland et al., 2008; Rolland et al., 2010), population growth rate (Rolland et al., 2009b) and survival of inexperienced adults (Nevoux et al., 2007) found in earlier studies was not included in our projected model. A negative association of warm SST on breeding success was identified by the modeling framework applied in Ch. 4 (Table 4.1). However, the

relationship with SST during the incubation period had a greater impact on the agreement of the observed data with the modelled data and the addition of the impact of wintering ground SSTs on breeding success did not significantly improve the model. It is possible that including this relationship would result in an even greater decrease in juvenile in addition to adult survival, producing a more rapid decline in this population. Additionally, though our projections assuming a positive relationship of warming SST during the breeding period are in line with previous findings (Rolland et al., 2008, 2009a; Rolland et al., 2010), the potential for a nonlinear relationship (Barbraud et al., 2011), which was not explored in the current analysis, could alter the implications of climate change for the population. For example, an exploration of non-linear (power) relationships of the environment with chick survival for Shy albatross breeding on Albatross Island, Tasmania, Australia within the same model framework presented here found large differences between projections based on the assumed power relationship (Thomson et al., 2015).

The interactions of environmental variation and fisheries on other albatross populations indicate colony-specific relationships and interactions shape population trends. For example, in a study directly comparing Kerguelen BBA with other albatross colonies, the focal colony stands out from wandering and sooty albatross breeding on Crozet, and yellow-nosed albatross (YNA) from Amsterdam Island as the only population where breeding success and adult survival was related to a fishery and environmental covariate (Rolland et al., 2010). Despite being positively impacted by regionally warming SSTs, the small population size of Amsterdam albatross breeding on Amsterdam Island makes the stability of this population highly sensitive to very small changes in bycatch (Rivalan et al., 2010). Other colonies breeding on low-lying islands, such the Northwestern Hawaiian Islands, face the additional threat of sea-level rise (Reynolds et

al., 2012). Additionally, disease outbreaks within the YNA colony on can significantly impact chick mortality and fledging success (Rolland et al., 2009a). Therefore, the relationship of climate change with disease outbreaks may significantly impact the viability of this population. The major threats to albatross populations are often colony specific and the management options to address these threats will require case-by-case consideration.

5.5.2 Continued development and applications

These findings demonstrate the value of considering the impacts of climate change on both albatross and fleet dynamics. Despite the relatively small projected impact of bycatch on this population, the ability to test different scenarios for effort provides increased flexibility in the design and assessment of potential management approaches. While fleet dynamics have recently been used to assess bycatch mitigation options within national boundaries (Mangel et al., 2015; Pascoe et al., 2013) there is a clear need to bridge the gap in information between national (Dowling et al., 2012; Pascoe et al., 2013) and high-seas fishing effort. This could be achieved by collaborating with Regional Fisheries Management Organizations and the fleets themselves. The resolution of the albatross population model could be improved by incorporating greater temporal variability in the spatial distribution of projected fishing effort, as well as at-sea distributions of albatrosses. Others have used albatross habitat preferences to estimate interaction with fisheries (Žydelis et al., 2011). As shifts in the at-sea distribution of albatross have already occurred (Weimerskirch et al., 2012); incorporating projected shifts could enhance the value of resulting projections. The inference from these types of models is already being used to assist managers making important decisions regarding mitigation of both bycatch and the environmental impacts of climate change (Alderman and Hobday, in press). Continued

assessment and development of integrated population models is essential to support informed management decisions in the face of climate change.

5.6 Acknowledgements

We are particularly grateful to all the field workers involved in the monitoring program over the past 40 years on the black-browed albatross at Cañon des Sourcils Noirs, Kerguelen Islands. The present work was supported financially and logistically by the Institut Polaire Français Paul Emile Victor (program 109), Terres Australes et Antarctiques Françaises, Zone Atelier de Recherches sur l'Environnement Antarctique et Subantarctique (CNRS-INEE), and has been approved by the ethics committee of IPEV and by the Comité de l'Environnement Polaire. We also thank Sophie Jeudi de Grissac and Henri Weimerskirch (CNRS-CEBC) for sharing and providing guidance on the use juvenile albatross distribution at-sea data. We thank D. Besson for the data management. We thank all of the organizations and individuals whom enabled or provided access to fisheries data. In particular, we thank the Service des Pêches des Terres Australes et Antarctiques Françaises and the contrôleurs de pêche for collecting the trawl effort data in the Kerguelen EEZ, and Guy Duhamel (resp.), N. Gasco, A. Martin, P. Pruvost and C. Chazeau for the management of the Pecheker database. Miguel Herrera and Gerard Domingue (IOTC) provided guidance on the use the data.

6 Implications and opportunities to manage in the face of climate change

Outlook for Kerguelen black-browed albatross and Japanese and Taiwanese pelagic longline fleets

The winners and losers of climate change will be determined through a balance of multiple interactions. The models developed here build on each other, and predict that the BBA colony at Cañon des Sourcils Noirs on Kerguelen is likely to slowly decline. This projected decline is attributed to density-dependent increases in juvenile and immature mortality rates as the result of increased chick survival due to increasing SST near the colony. While the positive relationship between breeding success and SST has been identified in earlier studies (Rolland et al., 2008; Rolland et al., 2009b; Rolland et al., 2010), this initially counter-intuitive impact on the number of breeding pairs is a novel insight. The future bycatch in this population is projected to be very low, in part due to the assumed cessation of IUU demersal longline effort near the colony. This fleet is implicated as the driving force of the observed decline in this population from the mid-1990s to the mid-2000s (Ch. 4), from which the population appears to have nearly recovered.

The projected decrease in Japanese and Taiwanese pelagic longline effort is in agreement with observed patterns in a reconstruction of historic effort (Pauly and Zeller, 2016) and has already occurred in these fleets in the Atlantic sector of the Southern Ocean (Ch. 2). Indeed, concerns over the financial viability of large (> 24m) pelagic longline vessels and increasing numbers of smaller vessels offering greater flexibility in target species (Hamilton et al., 2011) may alter patterns of future fishing effort from poleward, open ocean regions towards costal and island communities. While this would result in altered interactions near these communities, it

would reduce the probability of bycatch for seabirds breeding on remote, poleward islands, including Kerguelen.

Alternate assumptions could produce alternate trajectories

These results suggest that BBA on Kerguelen will slowly decline, despite a projected low impact of bycatch. However, alterations to key assumptions in the projected models could produce an alternate trajectory or implicate different threats. For example, if the relationship with SST and chick survival is non-linear, as has been found by Barbraud et al. (2011), the projected increase in chick survival could plateau at a different rate or reverse its trend, altering the intensity of density-dependence on juveniles and immature in subsequent years and therefore the population trajectory. Using the same integrated model framework, opposing projected trajectories were found by Thomson et al. (2015) depending on whether linear and non-linear relationships between the environment and chick survival were used. Including the moderately significant addition of the negative impact of warming SST in the wintering grounds prior to breeding (Table 4.1) in the albatross population model could alter the projected future for this colony. The potential impact of fisheries on food abundance is known to impact other seabirds (Frederiksen et al., 2004) and could impact Kerguelen BBA in the future, but was not assessed in this study. Additionally, given recent findings of wandering albatross from Crozet identifying a 5° pole-ward shift in the historic at-sea distribution (Weimerskirch et al., 2012), developing and incorporating a distribution at-sea model into the population dynamics model projections could provide greater insight into the potential future bycatch.

Regarding effort projections, assuming that the future Japanese and Taiwanese pelagic longline fleets maintain the same strategy and targeting as in the recent past quite likely

underestimates their flexibility. Both fleets have been active in the Southern Ocean for over 60 years and have altered their behavior in response to new markets, technologies, and regulations (Hamilton et al., 2011; Moreno and Herrera, 2013). Allowing projected future versions of these fleets to change their fishing strategy and shift between known, or develop new, target species would be more realistic. Likewise, the projected static distribution of all other pelagic, and all demersal longline, and trawl fleets provides a narrow assessment of their role in the future ocean (Plagányi et al., 2011)

Broader application of fleet dynamics modeling

Given the impact of fishing effort on both target and bycatch populations, there is a clear need to understand the factors impacting where, when, and how fishers decide to fish. Models of fleets within national waters are increasing, for both trawl (Gillis et al., 1995; Pelletier et al., 2009; Poos et al., 2010; Venables et al., 2009) and longline (Dowling et al., 2012; Mangel et al., 2015; Pascoe et al., 2013). One of the challenges in modeling high-seas effort is an incomplete understanding of the business model for each fleet. In addition to economic indicators, collaborations with social scientists and the fishers themselves could identify important human factors motivating fisher behavior at a fine scale to produce broad-scale consequences (Fulton et al., 2011; Van Putten et al., 2012). Incorporating more human motivations into fleet dynamics models, their application beyond national EEZs, and into different fleets is an essential layer to make informed predictions for our future oceans.

Managing through behavior

The ability to effectively manage populations requires an understanding of how different factors impact the population and system in question. This is enabled through collaborations and long-lived, respectful working relationships across cultures (Alexander et al., 2011; Nevins et al., 2009), research disciplines, and political and institutional structures (Maury et al., 2013; Salinger and Hobday, 2013). This promotes the ability to efficiently communicate and adaptively manage systems as new information arises and the systems themselves change (Plagányi et al., 2011).

However, managing effectively also requires the ability to influence and alter the behavior of the interacting factors, or the sensitivity to those factors, or both. In many circumstances, this involves explicit consideration of human behavior. For example, identifying the factors motivating fishers can enable managers to identify incentives which would benefit the ecosystem, providing fishers a choice instead of a mandate (Mangel et al., 2015; Pascoe et al., 2013).

Another approach to addressing the impacts of climate change is to actively enhance the focal population's resilience to change through intervention. Detailed guidance on designing conservation strategies (Mawdsley, 2011), developing adaptation options (Hobday et al., 2014), and methods for prioritizing options (Hobday et al., 2015b) are currently available. Furthermore, a case study applying an intervention option in a climate change threatened albatross colony demonstrates that intervention is a practical and valuable management tool (Alderman and Hobday, *in press*). Increasing awareness and communication to public and political outlets regarding the standardization of conservation strategy selection and the current applications of intervention strategies could reduce the current perception of these strategies as untested and therefore risky (Tam and McDaniels, 2013).

Effective management of the complex systems we rely on requires considering the full range of management tools, efficient transfer of information, and nimble response to changing conditions. To expedite knowledge exchange, enhance predictive capacity, and augment the ability to respond, it is essential to foster cross-cultural and cross-sectoral partnerships (Alexander et al., 2011; Maury et al., 2013; Nevins et al., 2009; Salinger and Hobday, 2013).

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